Resilience and stability of *Ecklonia radiata* kelp forests: the importance of intraspecific facilitation and patch dynamics

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"The number of living creatures of all Orders, whose existence intimately depends on the kelp, is wonderful. A great volume might be written, describing the inhabitants of one of these beds of sea-weed…I can only compare these great aquatic forests in the southern hemisphere with the terrestrial ones in the intertropical regions. Yet if in any country a forest was destroyed, I do not believe nearly so many species of animals would perish as would here, from the destruction of the kelp."

Charles Darwin, 1834, Tierra del Fuego, Chile

Cover: *Ecklonia radiata* kelp forest at Fortescue Bay, Tasmania. Photo by Matthew Doggett

This thesis is dedicated to all the volunteers who assisted on this project, underwater and on land, in the lab and in the field. This research and thesis would not have been possible without your commitment, humour, and contributions. Thank you.

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Statement of co-author contributions

Chapters 2–5 of this thesis have been prepared as manuscripts for submission to peer-reviewed journals. The design and implementation of the research, development of methodologies, data analysis, interpretation of results, and preparation of the manuscripts was the responsibility of the candidate but was carried out in consultation with supervisors and other co-authors. These contributions are outlined for each chapter below.

Chapter 2 – Sub-canopy abiotic conditions in kelp habitats depend on patch size

Craig Johnson and Jeffrey Wright contributed to the conception and design of the experiment, and analysis and interpretation of the results. Matthew Cameron contributed to development of methodologies and, along with Masayuki Tatsumi and Victor Shelamoff, contributed to implementation of the field research. All co-authors provided comments on the manuscript.

Chapter 3 - Press perturbation causes collapse of recruitment in a fragmented kelp forest

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Craig Johnson, Jeffrey Wright and Catriona Hurd contributed to the design of the experiment, and analysis and interpretation of the results. Catriona Hurd also supplied specialist equipment for the laboratory component of the study. Matthew Cameron and Victor Shelamoff contributed to the implementation of the field research, and Pamela Fernandez contributed to the implementation of the laboratory research. Damon Britton contributed to analysis and interpretation of results. All co-authors provided comments on the manuscript.

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Abstract

Kelp forests dominate coastal environments in temperate and subpolar latitudes around the world and, much like terrestrial forests, create complex habitats that support diverse and productive food webs. Studies of the resilience and stability of habitat-forming ecosystem engineers such as kelp have typically focussed on the role of external factors such as disturbance. Here, I propose that the stability and resilience of these species are also strongly influenced by internal processes. Such that, changes to the environment caused by engineer species positively affect their own demography (e.g. growth, survivorship), resulting in intraspecific facilitation via an 'environment-engineer' feedback.

Ecklonia radiata is the most widespread and abundant habitat-forming kelp in Australasia. Unfortunately, this species is threatened by increasing ocean temperatures, overgrazing, and pollution, and is consequently becoming increasingly patchy and sparse in many locations. Existing research has focussed on understanding how external stressors and disturbances influence the population dynamics of *E. radiata*, however internal drivers such as the environment-engineer feedback are potentially just as important but remain largely unaddressed. My core aims were to determine (i) how engineering of the local environment by *E. radiata* changes with patch size, and how this influences environment-engineer feedback on the species' demography, and (ii) how the nature of the feedback influences stability and resilience of *E. radiata* in the face of increasing habitat fragmentation and degradation.

Long-term field experiments confirmed that engineering of abiotic conditions within *E. radiata* habitats is patch size dependent (Chapter 2), and that reductions in patch size disrupt the recruitment of juvenile *E. radiata* (Chapter 3). These findings directed the construction of an artificial reef system spanning more than a hectare, and onto which over 500 adult *E. radiata* were transplanted. Using this unique experimental environment, I found that reductions to patch size and adult kelp density impair microscopic and macroscopic juvenile *E. radiata* due to a breakdown of ecosystem engineering by adult conspecifics, such that demographic collapse occurs in the absence of sufficient adult *E. radiata* (Chapter 4).

Two key outcomes from these field studies were: (1) the provision of suitable habitat and amelioration of physical stressors via ecosystem engineering by adult *E. radiata* appears critical to juvenile conspecifics and; (2) formation and development of filamentous turf algae – which inhibit kelp recruitment – is a primary cause and effect of the demographic collapse of *E. radiata* populations.

Ecklonia radiata and turf algae habitats exist as alternative stable states, with each state inhibiting the formation of the other. I developed an innovative laboratory experiment to improve understanding of how turf algae may disrupt the recruitment of *E. radiata*, and found that turf algae

create highly modified chemical conditions in the benthic microenvironments with elevated concentrations of oxygen and pH relative to *E. radiata* assemblages (Chapter 5).

Ultimately, this thesis presents results consistent with the hypothesis that positive environment-engineer feedback facilitates the demography of *E. radiata*. Moreover, the impaired ability of *E. radiata* to engineer change due to reductions in patch size cause a breakdown in this intraspecific facilitation, leading too reduced habitat stability and resilience. This work contributes to ecological theories of habitat resilience, facilitation, alternative stable states and ecosystem engineers, and provides insights for the future management, conservation and restoration of critically important kelp forest ecosystems.

Chapter 1. Introduction

Marine ecosystems around the world are under increasing pressure from anthropogenic stressors such as urban development, pollution and climate change (Airoldi & Beck 2011; Krumhansl et al. 2016; Hughes et al. 2017). One critical effect of these stressors is to reduce the extent and abundance of habitat-forming species or 'ecosystem engineers' such as coral, kelp, mangroves and seagrass (Ward et al. 2016; Wernberg et al. 2016; Hughes et al. 2017). These species are of disproportionate importance to ecosystem health and functioning because they create physically complex habitats with a range of microenvironments that support biodiverse and productive communities (Jones et al. 1994, 2010; Romero et al. 2015; van der Zee et al. 2016). In some cases, stressors can trigger declines in ecosystem engineering to the extent that complex and diverse ecosystems undergo 'phase shift' to become structurally simple, less diverse and less productive environments (Ling et al. 2009; Mumby 2009; Fung et al. 2011; Filbee-Dexter & Wernberg 2018). It follows that the future management and conservation of marine environments requires a thorough understanding of the resilience and stability of ecosystem engineers.

Ecosystem engineers modify their local environment in three main ways: structural engineering (changes in habitat structure, e.g. provision of physical complexity); abiotic engineering (changes to the abiotic conditions, e.g. light, water flow); and biotic engineering (changes in biota as a response to structural or abiotic engineering) (Jones et al. 2010). These modifications of the local environment have major consequences for the broader ecological community and can alter resource flows (Jones et al. 1997), influence invasion dynamics (Cuddington & Hastings 2004), ameliorate physical stressors (Crain & Bertness 2006), and promote biodiversity (Romero et al. 2015).

Studies of the resilience and stability of ecosystem engineer species have typically focussed on the role of external factors such as disturbance (Paine & Levin 1981; Johnson & Mann 1988; Dayton et al. 1992; Mumby 2009). However, the population dynamics of these species are also likely to be strongly influenced by internal processes, such that the environmental modifications caused by engineer species affects its own demography (e.g. recruitment, survivorship, growth), via a so-called 'environment-engineer' feedback (Cuddington et al. 2009; Jones et al. 2010). For example, structural feedbacks will occur when the engineer creates living space for conspecifics (e.g. creation of reef structure by calcifying corals, Jones et al. 1997). Abiotic feedbacks will occur when the engineer is affected by the abiotic changes it causes (e.g. alleviation of heat-stress and desiccation by barnacle aggregations, Bertness 1989). Biotic feedbacks will occur when structural or abiotic engineering modifies interactions between the engineer and other species (e.g. physical abrasion by kelp lamina excludes herbivores from the sub-canopy (Konar & Estes 2003). Intraspecific facilitation arising from

these feedbacks is likely apply to many habitat-forming species that reproduce, recruit, and grow in the engineered habitat.

However, environment-engineer feedbacks are likely to be complex. Firstly, the multiple pathways by which feedbacks can occur (i.e. structural, abiotic, biotic) creates potential for additive or synergistic effects among the separate mechanisms. Secondly, considering the importance of patch size in influencing fundamental community properties (Sousa 1984; Wright et al. 2004; Dunstan & Johnson 2006), and that ecosystem engineering can be density-dependent (Wernberg et al. 2005), it follows that environment-engineer feedbacks are also likely to be patch size and density dependent. Lastly, ecosystem engineering is likely to be context-dependent, varying with the environmental conditions (Jones et al. 2010). Context-dependency might arise if gradients in abiotic factors influence patch dynamics (adult density or patch size, Sousa 1984; Wernberg et al. 2011) and/or if engineering effects of abiotic factors become more important in more extreme environments (Crain & Bertness 2006; Bennett et al. 2015). While the complexity related to environment-engineer feedbacks is recognised at a theoretical level, the consequences for species of these feedbacks have not been fully explored empirically.

Kelp[1] (Order Laminariales) forests dominate coastal environments in temperate and subpolar latitudes around the world, and much like terrestrial forests they create productive and complex ecosystems that support high levels of biodiversity and economic value (Steneck & Johnson 2014; Schiel & Foster 2015; Teagle et al. 2017). As ecosystem engineers, kelp provide habitat through their own physical structure and modify the local abiotic (e.g. light, sedimentation) and biotic (e.g. the composition and richness of the understorey community) environment (Kitching 1941; Dayton et al. 1984; Eckman et al. 1989; Wernberg et al. 2005; Flukes et al. 2014). Unfortunately, in numerous regions around the world kelp forests are in decline, with habitat degradation often first manifesting as reductions in patch size and adult kelp density (Johnson et al. 2011; Steneck & Johnson 2014; Krumhansl et al. 2016).

The kelp *Ecklonia radiata* is the most widespread habitat-forming macroalga in Australia, occurring at depths between ~2–60 m and from subtropical waters on the east and west coasts along the entire southern coastline (Marzinelli et al. 2015; Bennett et al. 2016). This stipitate kelp (*sensu* Dayton et al. 1984) rarely grows taller than 1.5 m, but creates dense and spatially complex habitats across Australia's Great Southern Reef, supporting high levels of biodiversity, endemism and economic value (Phillips 2001; Bennett et al. 2016). Like many kelp species, *E. radiata* is under

[1] The taxonomic definition of kelp is the large, brown macroalga belonging to the Order Laminariales. However, some authors (e.g. Steneck & Johnson 2014) argue for a broader functional definition of kelp that includes other Orders of large, brown habitat-forming macroalgae such as those from the Orders Desmarestiales and Fucales. For clarity, I utilise the taxonomic definition of kelp throughout this thesis, but I acknowledge the important contribution of these other habitat-forming species to subtidal macroalgal forests around the globe (see also Schiel & Foster 2006; Coleman & Wernberg 2017).

threat from rising ocean temperatures, overgrazing from herbivores, and urbanisation and pollution (Connell et al. 2008; Ling et al. 2009; Vergés et al. 2016; Wernberg et al. 2016). As a result, *E. radiata* has suffered range-contractions and habitat fragmentation at numerous locations across its range. As it stands, a major impediment to managing, conserving and restoring kelp ecosystems is poor knowledge of the mechanisms underpinning their stability and resilience (Schiel & Foster 2006; Evans et al. 2017).

Previous research into the resilience of *E. radiata* and other marine ecosystem engineers has focussed primarily on their response to external drivers such as disturbance or interspecific interactions (e.g. Kennelly 1987; Steneck et al. 2002; Toohey & Kendrick 2007; Flukes et al. 2014). However, internal drivers such as environment-engineer feedbacks may be equally important. Indeed, breakdown of intraspecific facilitation and positive engineer-environment feedbacks may explain the slow recovery of *E. radiata* observed after large-scale losses (e.g Kirkman 1981; Toohey et al. 2007; Connell et al. 2008). Existing research on *E. radiata* has established a number of demographic and engineering processes relevant to ecosystem engineering and potential feedback pathways. These include, positive density-dependence in adults (Schiel & Choat 1980); elevated recruitment after canopy loss (Kirkman 1981; Toohey & Kendrick 2007; Flukes et al. 2014); changes to local abiotic conditions such as light and pH beneath *E. radiata* canopies (Wernberg et al. 2005; Britton et al. 2016), and; changes to the associated biotic community arising from abiotic engineering (Kennelly 1989; Kendrick et al. 1999; Wernberg et al. 2005; Irving & Connell 2006). However, there also remains a number of important knowledge gaps. For example, there have been few demographic studies of the microscopic life stages of *E. radiata,* particularly examining the factors affecting recruitment and survival of these life stage *in situ* (but see Tatsumi & Wright 2016). This is despite recognition that knowledge of the entire kelp life cycle is critical to understanding resilience (Reed 1990; Schiel & Foster 2006). Moreover, little is known about how patch dynamics influence the engineering capacity of *E. radiata* and resilience of the kelp ecosystem as a whole.

Thesis structure

The central aims of this thesis were to determine: (i) how engineering of the local environment by *E. radiata* changes with patch size and kelp density, and how this influences the species' demography via the environment-engineer feedback, and; (ii) how the nature of the feedback is likely to influence the stability and resilience of *E. radiata* in the face of habitat fragmentation and degradation. These aims were addressed using long-term field experiments (Chapters 2, 3, 4) and a combined lab-field experiment (Chapter 5).

Chapter 2. Sub-canopy abiotic conditions in kelp habitats depend on patch size

It was tested whether reductions in the size of *E. radiata* patches affects the species' capacity to engineer the abiotic environment within the sub-canopy. In an initially intact stand of *E. radiata,* patch size was manipulated over 12 months to simulate the effects of habitat fragmentation caused by anthropogenic stressors. Irradiance, kelp scour, water flow and sedimentation were then quantified within the sub-canopy environment across the range of patch sizes (0.1–2025 m^2), and the findings discussed in the context of how reductions in patch size of *E. radiata* may influence the associated biotic community – including the juvenile *E. radiata* that settle and develop within the sub-canopy environment.

Chapter 3. Press perturbation causes collapse of recruitment in a fragmented kelp forest

Reductions to *E. radiata* patch size, and subsequent changes to biotic and abiotic conditions in the sub-canopy, may be of particular importance if they interrupt mechanisms that support the species' demography, such as a positive environment-engineer feedback. Using the series of experimental patches outlined in Chapter 2, the effects of habitat fragmentation on the demography of the juvenile life stages of *E. radiata* were examined. Over 24 months, the density of juvenile and adult *E. radiata* within each patch was monitored and microscopic and macroscopic juvenile kelp sporophytes transplanted into each patch. Together with the findings from Chapter 2, this enabled analysis of how reductions in adult patch size influence the demography of juvenile *E. radiata*.

Chapter 4. Resilience and stability of kelp forests: the importance of patch dynamics and environment-engineer feedbacks

The results and experiences from the field experiments from Chapters 2 and 3 led to development of a novel, large-scale field experiment. A natural but controlled environment was required to explore fully how patch size and adult kelp density influence the environment-engineer feedback in *E. radiata*. So, in isolation from nearby natural reefs (~1.5 km away), an array of artificial patch reefs of various sizes and supporting adult *E. radiata* transplanted at different densities was established over an area of ~1.5 ha. This unique experiment allowed examination of whether breakdown of positive environment-engineer feedback caused by habitat degradation (i.e. reductions in patch size and adult density) influences the stability and resilience of *E. radiata* habitats. Specifically, it was determined how sub-canopy abiotic conditions on experimental reefs changed with patch size and adult kelp density, and how these changes affected fundamental demographic processes of both microscopic and macroscopic juvenile *E. radiata* (i.e. recruitment, survivorship and growth).

Chapter 5. Chemical microenvironments within macroalgal assemblages: implications for the inhibition of kelp recruitment by turf algae

Observations and findings from the previous experiments informed development of a combined lab and field experiment, which focussed on the mechanism behind poor recruitment of *E. radiata* within the turf algae-sediment matrices that form in degraded sub-canopy environments. It is well recognised that turf algae inhibit kelp recruitment, however relatively little is known about the precise mechanism(s). One possible influencing factor is the chemical environment within the turf-sediment matrices and into which the kelp propagules settle and develop. Thus, the chemical microenvironments (i.e. O_2 concentration and pH at scales of 0.1–50 mm) within different macroalgal assemblages (including a natural turf-sediment matrix and a kelp-dominated assemblage) were characterised and compared. These microprofiles were then used to assess whether the chemical microenvironments within turf algae might inhibit kelp recruitment and contribute to stability and resilience of the alternative states of turf- and kelp-dominated habitats.

Chapter 6. General Discussion

Here, I briefly summarise the overall findings of the thesis, before discussing the combined results and their broader implications in the context of ecological theories of facilitation, stress gradients, and niche space. Key areas of focus for future kelp research that were suggested from the results of this project are also discussed – including the importance of considering positive environment-engineer feedbacks to the ecological restoration of kelp forests.

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Chapter 2. Sub-canopy abiotic conditions in kelp habitats depend on patch size

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Abstract

Environmental degradation from anthropogenic stressors may alter fine-scale physical conditions within habitats, with potential consequences for the associated biodiversity and habitat resilience. These changes may be of particular importance if they influence the stability and resilience of habitat-forming species such as kelp. We manipulated patch size of the kelp *Ecklonia radiata* to simulate habitat fragmentation caused by anthropogenic stressors, and assessed how sub-canopy conditions including irradiance, kelp scour, sedimentation, and water flow varied with patch size. While effects differed in magnitude and by season, the overall pattern was that reductions in patch size resulted in increased sub-canopy irradiance, sediment accumulation and water flow, and decreased sediment deposition and kelp scour. We demonstrate that abiotic conditions beneath the *E. radiata* canopy depend on patch size, and that the capacity of the canopy to engineer abiotic change is impaired in small patches due to fewer individuals and greater influence of the patch edge on the sub-canopy environment. Since the local physical environment is a strong predictor of sub-canopy assemblage structure in *E. radiata* habitats, it is likely that reductions in patch size will alter the composition of sub-canopy communities. Ultimately, these abiotic and biotic changes may have consequences for the juvenile kelp that settle and develop within the sub-canopy, and therefore influence the broader stability of this important habitat-forming species and the associated biodiversity.

Introduction

A fundamental goal of ecology is to understand the relationship between organisms and the physical environments they inhabit (Kitching et al. 1934; Andrewartha & Birch 1954). This is becoming increasingly relevant as the organisation and distribution of species are altered due to climate change and other anthropogenic forces (Hoegh-Guldberg & Bruno 2010; Pecl et al. 2017). This 'redistribution of biodiversity' is typically driven by broad scale changes to physical environmental conditions, such as temperature or available resources (Poloczanska et al. 2013; Lenoir & Svenning 2015; Pecl et al. 2017). However, anthropogenic stressors may also induce changes in physical conditions at finer spatial scales within habitats (e.g. reductions in terrestrial forest patch sizes due to logging can cause reductions in soil moisture due to edge effects, Murcia 1995), and although it has received less attention this too may contribute to the reorganisation of species (Fischer & Lindenmeyer 2007). These fine-scale changes may be of particular importance in biogenic habitats, such as coral reefs and kelp forests, where altered physical conditions that disturb the habitat-forming species are likely to have consequences for stability and resilience of the wider ecosystem (Mumby 2009; Jones et al. 2010; Wernberg et al. 2016).

Kelp (Order Laminariales) and many other large brown macroalgae (e.g. Order Fucales) are ecosystem engineers (*sensu* Jones et al. 2010) that create habitat through their physical presence, but also modify abiotic conditions such as light, sedimentation and water flow (e.g. Wernberg et al. 2005). Kelp forests dominate coastal environments in temperate and subpolar latitudes around the world (Steneck et al. 2002; Krumhansl et al. 2016) and, much like terrestrial forests, create spatially complex habitats that support diverse and productive food webs (Kitching et al. 1934; Graham et al. 2007; Teagle et al. 2017). However, in many places kelp forests are under threat from rising ocean temperatures, overgrazing from herbivores, and eutrophication (Graham et al. 2007; Johnson et al. 2011; Krumhansl et al. 2016). A major consequence of this degradation is that many kelp habitats are becoming increasingly degraded and fragmented (Steneck et al. 2008; Krumhansl et al. 2016; Wernberg et al. 2016).

Habitat fragmentation typically involves loss of habitat, reductions in patch size, and increases in distance between patches of remaining habitat (Murcia 1995; Fischer & Lindenmeyer 2007). Widespread loss of kelp forest habitat at regional-scales would have far-reaching consequences for coastal biodiversity and productivity (Graham et al. 2007; Bennett et al. 2016). At finer scales, loss of kelp is also likely to impact the ecological community due to a reduction in the structure available for recruitment (Deza & Anderson 2010; Hinojosa et al. 2014) and habitation (Perez-Matus & Shima 2010; Teagle et al. 2017). However, the effects of habitat loss may not be analogous to those caused by reductions in patch size. This is because reductions in patch size alter fundamental properties of the habitat by increasing the ratio of patch edge to interior and may therefore affect

abiotic conditions within the habitat (Dayton et al. 1984; Sousa 1984; Murcia 1995). Here we examine how reductions in patch size of a dominant habitat-forming kelp affects its ability to modify the sub-canopy abiotic environment.

Ecklonia radiata is the most widespread and abundant habitat-forming kelp in Australasia. This stipitate kelp (*sensu* Dayton et al. 1984) rarely grows taller than 1.5 m, but creates dense and complex habitats with defined sub-canopy environments and levels of productivity equal to many larger kelp species (Larkum 1986: Hatcher et al. 1987). The Great Southern Reef – Australia's continental wide temperate reef system – is dominated by *E. radiata* and supports high levels of biodiversity and endemism (see Bennett et al. 2016). Kelp habitats in Australia are under threat from coastal development, ocean warming and range-extending herbivores, and subsequently are becoming increasingly patchy and sparse in many regions (Ling 2008; Bennett et al. 2016; Vergés et al. 2016; Wernberg et al. 2016). Despite high natural variability at local scales (Kendrick et al. 1999; Marzinelli et al. 2015), physical conditions beneath *E. radiata* canopies are strong predictors of community composition and assembly (Kendrick et al. 1999; Irving & Connell 2006a; Toohey 2007). The effects of abiotic factors such as irradiance and kelp scour on understorey species and communities have also been widely tested and have well recognised responses (also see Kennelly 1989; Connell 2003; Wernberg et al. 2005). However, it is unclear how habitat fragmentation will affect these local-scale physical conditions within *E. radiata* habitats. Understanding these processes will help fill knowledge gaps critical to the future management and conservation of kelp forest ecosystems in Australia and around the world (Schiel & Foster 2006; Steneck & Johnson 2014).

We manipulated patch size of *E. radiata* and examined whether habitat fragmentation altered abiotic conditions within the sub-canopy. By maintaining the experimental treatments for 12 months we simulate the persistent effects of habitat fragmentation caused by anthropogenic stressors. In the centre of these patches, ranging from 0.1–2025 m^2, we quantified sub-canopy irradiance, kelp scour, water flow and sedimentation, and as an indicator of environmental stability, investigated whether variance of these factors changed with patch size. Ultimately, we explore how the capacity of *E. radiata* to engineer abiotic change is affected by reductions in patch size and what effect this may have on the sub-canopy community – including the juvenile *E. radiata* that settle and develop in the sub-canopy environment.

Methods

Study site

The study site was located within Fortescue Bay in southeast Tasmania, Australia (-43.13735, 147.96819, Fig. 2.1). The site is semi-exposed and subject to occasional ocean swell, with dolerite

reef dominated by *E. radiata*. Flukes et al. (2014) provide a detailed description of the macroalgae community at the site.

In February 2014, ten approximately square patches (0.1, 0.3, 0.9, 2.7, 9, 25, 73, 225, 676 and ~2025 m^2) were established within a largely continuous stand of *E. radiata* at a depth of 13.9 ± 0.1 m (SE, n = 10). This range of patch sizes allowed detection of potential critical thresholds at small patch sizes and steady progression up to the largest patch size, which as a continuous stand of *E. radiata* acted similar to a control treatment. Divers using SCUBA created the patches by clearing all canopy-forming macroalgae (i.e. any species with adults >300 mm in height) from a 2 m wide 'buffer' around the measured patch perimeter. This distance is larger than even the longest *E. radiata,* and thus ensured patches were physically isolated from the surrounding stand of kelp. Buffer areas were maintained every 6 weeks and any new canopy-forming algae removed. The largest patch did not have a buffer as it was a naturally isolated (by sand) patch reef. Giant kelp, *Macrocystis pyrifera*, were not cleared at any time throughout the experiment as it is a threatened species in Australia; however, we only observed seven individuals over the length of the study and none larger than ~500 mm.

The experimental patches consisted almost entirely of a monospecific canopy of *E. radiata* (14.5 ± 2.5 kelp m^{-2}, SE), although some of the larger patches (i.e. >70 m^2) contained small areas (<2 m^2) with fluctuating cover of bare substratum or *E. radiata* intermixed with the canopy-forming *Cystophora monilifera* or *Phyllospora comosa* (both Order Fucales). The patches were all situated in areas of similar reef profile, exposure, turbidity, tidal current, community structure etc. Patches were separated from each other by at least 5 m, except in one instance where due to reef bathymetry it was necessary for two patches to have an adjoining buffer on one side (i.e. 4 m separation). All visible *Centrostephanus rodgersii* urchins were removed from the patches and buffer areas at the beginning of the experiment (~570 individuals), as destructive overgrazing by this species could influence the experimental treatments (Ling 2008). Patches were maintained for a complimentary experiment (see Chapter 3) for 12 months prior to beginning measurements of abiotic factors.

Abiotic measurements

Sediment deposition

Sediment deposition was measured using sediment traps constructed from PVC piping. Each trap was cylindrical (300 x 50 mm, L x D) and had a baffle installed across the opening. The baffle and length-diameter ratio of 6:1 ensured trapping efficiency and minimised likelihood of captured sediments being resuspended (Jürg 1996). Sediment traps were installed during autumn (March), winter (June), spring (September) and summer (January) for a period of 44 days (± 1 day, SE).

Sediment traps were positioned in the approximate centre of each patch, with two positioned above the kelp canopy and two below. Above-canopy traps acted as controls and measured ambient rates of sediment deposition, while sub-canopy traps measured treatment effects. For collection, sediment traps were sealed underwater before being retrieved to the surface and transported to the lab. Trap contents were flushed into pre-weighed foil trays and dried at 70ºC until constant mass (~48 hours). The dried contents were weighed on a laboratory balance to 0.01 grams and a rate of sediment deposition above and below the kelp canopy in each patch calculated based on the mean dry mass of the sediment from the two traps in each position (g day^{-1} m^{-2}). When a trap was lost or unsuitable for analysis (e.g. due to octopus habitation), sediment mass was calculated from the single trap. Dry sediments were sieved through 250 and 62 μm mesh to examine their composition.

Sediment accumulation

The depth of accumulated sediments covering the substratum was measured to the nearest 1 mm using a small ruler at 2–8 random locations within each patch (depending on patch size, see Table 2.1). Sediment accumulation was measured in autumn (March), winter (June), spring (September) and summer (January).

Water flow

The dissolution of clod cards (plaster blocks) was used to assess relative differences in sub-canopy mass transfer. For the sake of communication, mass transfer is hereafter referred to as water flow, but we acknowledge the difference of these processes (see Thompsen & Glenn 1994; Porter et al. 2000). Clod cards were made by mixing gypsum plaster ($CaSO_4$) and fresh water at the manufacturer's ratio of 10:7.5 plaster-water, and cast using silicon moulds. A 50 mm bolt, for installation, was embedded in each clod card before the plaster solidified. The clod cards were left to set for 24 hours and then dried at 50°C for a further 24 hours before being weighed. Clod cards were installed during autumn (March), winter (June), spring (September) and summer (February).

Each clod card was mounted to a thin plastic base and installed in the centre of each patch, either attached to the substratum or to a bracket atop the sediment trap array. These positions represented sub-canopy and above-canopy environments respectively. The clod cards positioned above the canopy acted as controls that measured ambient water flow, while those below the canopy measured treatment effects. All clod cards were fitted with a coarse mesh guard to protect them from the confounding effects of erosion due to kelp scour. After ~72 hours *in situ,* clod cards were collected and dried at 50° C for 24 hours, and then re-weighed. Due to inconsistencies in the plaster the initial masses of clod cards varied by ~15% and so mass loss was standardised as a percentage of mass lost. Preliminary testing revealed no relationship between initial mass and magnitude of mass lost.

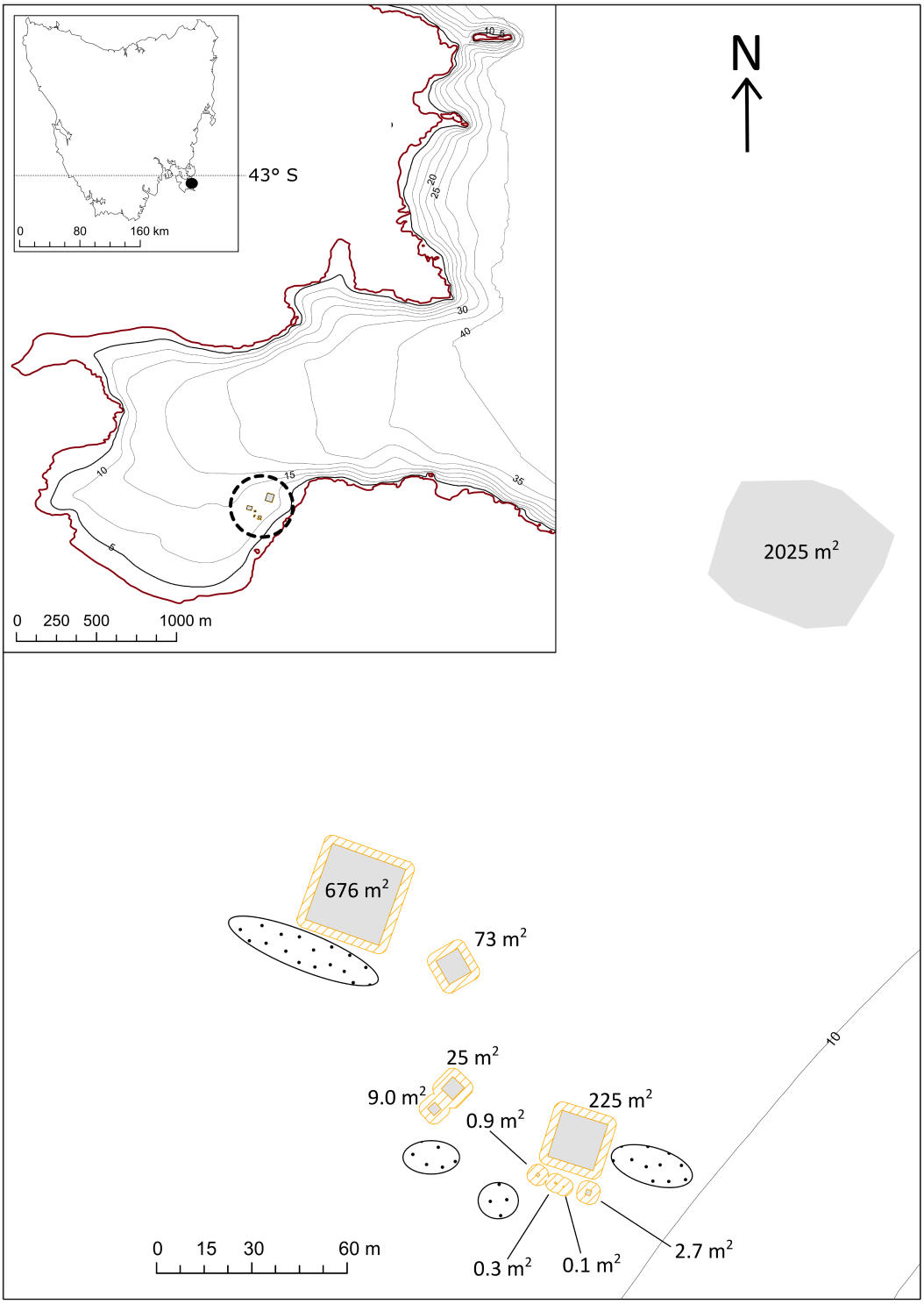

Figure 2.1. Schematic of the position of the experimental patches at the study site within Fortescue Bay, Tasmania (insets). Patches (shaded) were situated within a continous stand of *Ecklonia radiata* (not illustrated) but were isolated by creating a 2 m-wide cleared 'buffer' around each patch (depicted as hatched area). The largest patch (2025 m^2) did not have a buffer and was irregularly shaped because it was a naturally discrete section of reef. The black-dotted areas represent approximate locations of extensive *Centrostephanus rodgersii* urchin barrens.

Table 2.1 Experimental patches and number of replicate measures of sediment accumulation from each patch.

patch number	*patch size (m^2)*	*log_3(patch size) [$log_3(m^2)$]*	*number of sediment accumulation samples*
1	0.1	-2.10	2
2	0.3	-1.10	2
3	0.9	-0.10	4
4	2.7	0.90	8
5	9	2.00	8
6	25	2.93	8
7	73	3.91	8
8	225	4.93	8
9	676	5.93	8
10	2025	6.93	8

A wave-exposure model (Mundy & Keane, in prep.) was used to calculate daily wave energy at the study site over the 12-month period, which provided a seasonal and annual context to the short-term measurements of ambient water flow and kelp scour. The model incorporates wind and wave data (i.e. direction, height, period) from the Australian Bureau of Meteorology (BOM 2017) with local fetch lines and bathymetry to produce a site-specific mean daily wave energy index. The index required log-transformation due to massive peaks in wave energy from storms.

Scour

Scour, the physical abrasion caused by kelp lamina, was assessed using ceramic tiles (200 x 200 mm) coated with black water-based paint. The paint was easily removed when kelp laminae brushed the tile, and so the percentage of paint removed provided a relative measure of scour. Two tiles were installed in the approximate centre of each patch and left for ~72 hours. Tiles were photographed underwater immediately following installation and again at time of collection. Percentage paint loss for each tile was assessed using ImageJ (v. 1.48) and mean scour quantified for each patch. A pilot study revealed that tiles placed in areas free from kelp experienced negligible (<2%) paint loss over 72 hours. Scour was measured during autumn (March) and summer (January). Sampling was also attempted during winter and spring but abandoned due to inclement weather.

Irradiance

Photosynthetically Active Radiation (hereafter, irradiance) was measured using a LI-COR LI-1500 Light Sensor Logger and LI-193 Spherical Underwater Sensor. This 330 º spherical sensor allowed measurement of the incidental irradiance that enters through the sides of kelp patches. The sensor was secured to a 1.8 m pole to minimise diver interference, and irradiance in the centre of each patch recorded for 60 seconds above and below the kelp canopy. Irradiance was automatically logged every 15 seconds as mean µmol photon m^{-2} s^{-1}, providing four measures per position over the 60-second sample. Above-canopy measurements provided ambient irradiance and acted as controls,

while sub-canopy readings measured treatment effects. Irradiance was measured in autumn (March), winter (June), spring (September) and summer (February); although no data were obtained for the summer period due to equipment malfunction. During autumn and spring, sampling occurred between 1100–1400, and during winter between 0915–1100 (due to weather constraints).

Data analysis and statistics

Data were analysed using linear regression of abiotic factors against patch size. The variance (σ^2) of abiotic factors over the study period was analysed using linear regression and PCA. Test assumptions were assessed using diagnostic plots, model residuals and the Shapiro-Wilk normality test. Data that did not meet assumptions were transformed based on values of λ from Box-Cox plots, as noted in model output. The addition of a small constant was required to ensure appropriate transformation when the response variable was zero. Patch size was $\log_3$-transformed prior to testing since patch sizes were initially determined on an approximately $\log_3$ scale (see Table 2.1 for transformed patch sizes). Principle Component Analysis (PCA) was used for multivariate exploration of the abiotic factors. PCAs were based on correlation matrices and used mean measurements per patch to achieve a balanced design. PCA figures display patch numbers instead of patch size for clarity (patch numbers increase from 1 to 10 from smallest to largest; see Table 2.1). All tests were conducted with alpha at $\alpha = 0.05$ using *R* (v. 3.2.5; *R* Core Team) and the *MASS* and *lattice* packages. Figures are presented with untransformed response variables for clarity, and were produced using *ggplot2* (univariate), and *prcomp* and *ggfortify* (PCA) packages in *R*, along with *Inkscape* (v. 0.91).

Results

Water flow

There was no effect of patch size on the dissolution rates of clod cards positioned above the kelp canopy during any sample period (Appendix 2.1). Using these rates as the measure of ambient water flow, the summer period had the highest flows with above-canopy clod cards losing 46 ± 0.9 % (n = 10, SE) of their mass over the 72-hour period, compared to 20 ± 0.6 % (autumn), 21 ± 0.3 % (winter) and 15 ± 0.9 % (spring). This largely aligns with the modelled wave energy over the 72-hour sampling periods (Fig. 2.2), when mean daily wave energy were highest in summer (-6.55 ± 0.05), compared to autumn (-7.07 ± 0.55), winter (-7.85 ± 0.24) and spring (-7.59 ± 0.23).

Dissolution rates of sub-canopy clod cards relative to above-canopy clod cards were highly variable (Fig. 2.3). During the sampling periods in autumn, winter and summer, no significant effects of patch size were detected (Table 2.2). During the autumn and winter periods, there were indications of a quadratic response, and measures from each of the two smallest and two largest patches had high leverage on the overall regression (Fig. 2.3). Despite the poor fit, there was no justification to exclude

any patches from the analyses or to include a curvilinear model term (e.g. a second-order polynomial), and so the linear model was left unmodified.

During the spring sampling period, relative dissolution rates of sub-canopy clod cards – and hence water flow beneath the kelp canopy – did significantly decrease with patch size (Table 2.2). In patches larger than 2.7 m^2, flow was typically lower below the canopy than above it, and the lowest sub-canopy flow was recorded in the largest patch, where sub-canopy clod card dissolution was ~45% of that above the canopy. Patch size had no effect on the variance of sub-canopy clod card dissolution (Table 2.3, Fig. 2.4a).

Scour

During autumn, the percentage of paint removed from the tiles – and thus scour – increased significantly with patch size (Table 2.2). There was a similar but non-significant trend during summer, and on average, tiles had more paint removed during summer than autumn (Fig. 2.5). During both seasons, scour in patches smaller than 3m^2 was very low (typically less than 10% of the paint was removed over 72 hours). Patch size had no effect on the variance of scour in each patch (Fig. 2.4b, Table 2.3).

Irradiance

Above-canopy irradiance varied markedly across seasons: autumn = 235 ± 14; winter = 98 ± 4; spring = 153 ± 4 μmol photon m^{-2} s^{-1} (± SE, n = 40). During autumn and winter, above-canopy irradiance significantly increased with patch size (Appendices 2.1, 2.2). Dissipating cloud cover during autumn and the timing of measurements over the morning in winter, are the suggested causes of these spurious patterns. During spring, there was no relationship between patch size and above-canopy irradiance. To account for the differences in above-canopy light levels among patches, sub-canopy irradiance was expressed relative to the associated above-canopy measurement in each patch (Fig. 2.6). Nonetheless, results were similar in magnitude, direction and significance when using either relative or absolute values of sub-canopy irradiance.

Sub-canopy irradiance in autumn was quite variable, and often higher than the associated above-canopy reading (most likely due to the intermittent cloud cover), especially in the smaller patches (Fig. 2.6a). Nonetheless, relative sub-canopy irradiance decreased significantly with patch size during autumn (Table 2.2). Data in winter showed less variability, and no measures of sub-canopy irradiance were higher than the paired above-canopy measurement (Fig. 2.6b). As in autumn, relative sub-canopy irradiance during both winter and spring significantly decreased with patch size (Table 2.2). Variance in sub-canopy irradiance also declined significantly with patch size (Fig. 2.4c, Table 2.3). The three smallest patches were highly variable, while sub-canopy irradiance tended to stabilise in patches larger than 2.7m^2.

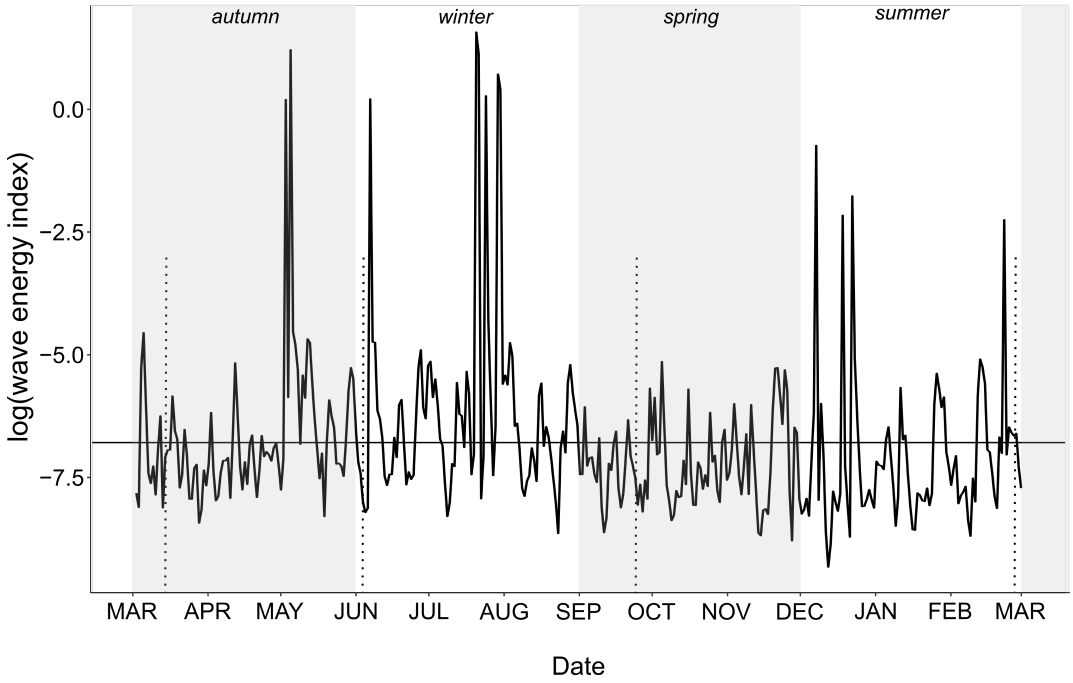

Figure 2.2 Seasonal variations in mean daily wave energy at the study site. Log-transformed wave energy indices from March 2015 until March 2016 were derived from a site-specific wave-exposure model (see Methods), with higher indices representing greater wave energy. The solid horizontal line is the mean annual wave energy index, and vertical dotted lines indicate the periods of clod card sampling during each season.

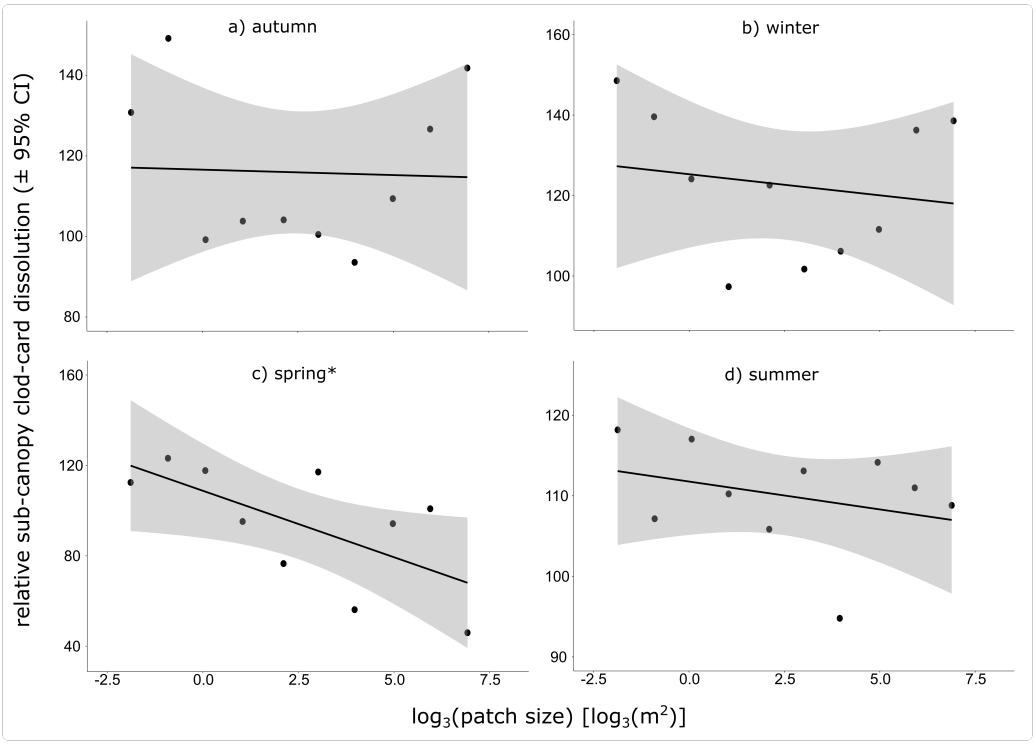

Figure 2.3 Effects of *Ecklonia radiata* patch size on sub-canopy water flow, measured as mean dissolution of plaster clod cards relative to the paired above-canopy clod card. Thus 100% represents equal rates of clod card dissolution below and above the kelp canopy, and values higher or lower than 100% indicate greater or less dissolution below the canopy, respectively. Measurements were taken during four seasons (a–d) at a depth of 14 m on reefs in Fortescue Bay, Tasmania, Australia. Note the different y-axis scales. Seasons with significant relationships ($P < 0.05$) are denoted with an asterisk.

Table 2.2 Linear regressions examining how sub-canopy abiotic factors vary with patch size within seasons. Response variables and associated transformation are noted in the first column. The factor, patch size, was $\log_3$-transformed to best meet test assumptions. Significant relationships denoted in bold and with an asterisk.

data analysed	*F-value*	*P-value*
WATER FLOW		
autumn $(Y)^{-2.25}$	$F_{(1,8)} = 0.003$	0.961
winter $(Y)^{1.10}$	$F_{(1,8)} = 0.257$	0.626
spring $(Y)^{2.25}$	$F_{(1,8)} = 6.304$	**0.036***
summer $(Y)^{9.00}$	$F_{(1,8)} = 1.421$	0.267
SCOUR		
autumn $(Y)^{-0.35}$	$F_{(1,8)} = 9.547$	**0.015***
summer $(Y)^{0.45}$	$F_{(1,8)} = 3.291$	0.107
IRRADIANCE		
autumn $(Y)^{0.20}$	$F_{(1,58)} = 17.545$	**<0.001***
winter $(Y)^{0.45}$	$F_{(1,38)} = 115.9$	**<0.001***
spring $(Y)^{0.60}$	$F_{(1,38)} = 200.59$	**<0.001***
SEDIMENT DEPOSITION		
autumn $(Y)^{0.50}$	$F_{(1,8)} = 0.896$	0.372
winter $(Y)^{0.70}$	$F_{(1,8)} = 0.556$	0.477
spring $\log(Y)$	$F_{(1,8)} = 3.334$	0.105
summer $(Y)^{-0.70}$	$F_{(1,8)} = 8.247$	**0.021***
SEDIMENT ACCUMULATION		
autumn $(Y+0.1)^{0.35}$	$F_{(1,8)} = 3.161$	0.113
winter $(Y+0.1)^{-0.50}$	$F_{(1,8)} = 1.792$	0.218
spring $(Y+0.1)^{0.60}$	$F_{(1,8)} = 23.248$	**0.001***
summer $(Y+0.1)^{0.15}$	$F_{(1,8)} = 2.299$	0.168

Table 2.3 Linear regressions examining how variance (σ^2) of the five abiotic factors differed according to patch size. Response variable and associated transformation is noted in the first column. The factor, patch size, was $\log_3$-transformed to best meet test assumptions. Significant relationships denoted in bold and with an asterisk.

data analysed	*F-value*	*P-value*
Water flow $(Y)^{-0.15}$	$F_{(1,8)} = 0.719$	0.421
Scour $(Y)^{0.25}$	$F_{(1,8)} = 2.981$	0.123
Irradiance $\log(Y)$	$F_{(1,8)} = 23.426$	**0.001***
Sediment deposition $(Y)^{-0.30}$	$F_{(1,8)} = 8.211$	**0.021***
Sediment accumulation $(Y)^{-0.10}$	$F_{(1,8)} = 12.889$	**0.007***

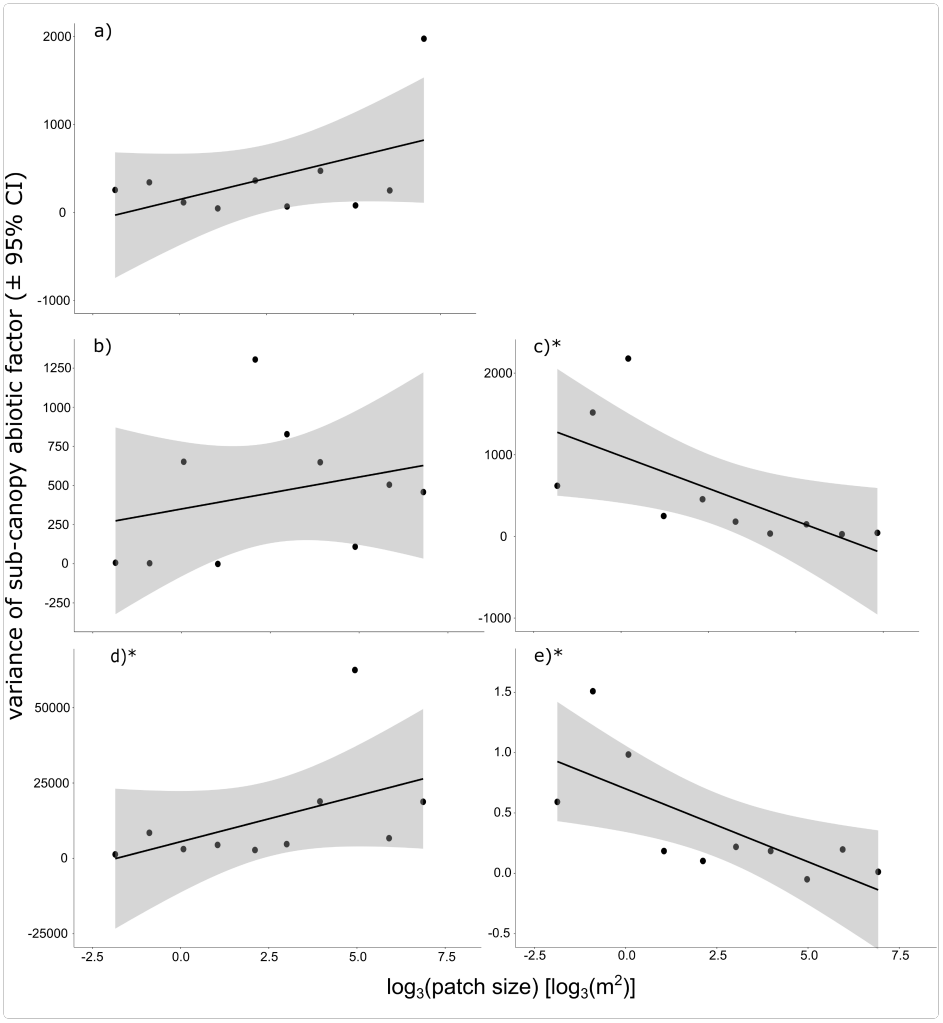

Figure 2.4 Effects of *Ecklonia radiata* patch size on the variability of five sub-canopy abiotic conditions; (a) relative clod card dissolution; (b) scour; (c) relative irradiance; (d) sediment deposition rates, and; (e) sediment accumulation. Note the different y-axis scales. Abiotic factors with significant relationships ($P < 0.05$) are denoted with an asterisk.

Sediment deposition

The collected sediments were mostly fine to very fine sand (250–62 µm) with some silt (<62 µm) and coarser sands (>250 µm). There was no relationship between rates of sediment deposition above the canopy and patch size during any season (Appendix 2.1). Ambient rates of sediment deposition differed widely across season and were by far the highest during summer (237 ± 42), compared to autumn (75 ± 9) winter (55 ± 7), and spring (26 ± 3) (data are means as g day^{-1} m^{-2} ± SE, n = 10). Qualitatively, there were no apparent differences in the sediment composition across seasons.

There was no effect of patch size on rates of sub-canopy sediment deposition during autumn, winter or spring (Fig. 2.7). However, rates of sub-canopy sediment deposition during summer increased significantly with patch size (Table 2.2, Fig. 2.7d). The variance of rates of sub-canopy sediment deposition in each patch also increased significantly with patch size (Table 2.3, Fig. 2.4).

Sediment accumulation

Free or unbound sediments in the experimental patches were rare. Instead, sediment particles accumulated within algae turfs (consisting mostly of filamentous green or red algae) growing on the rocky substratum to form a semi-consolidated turf-sediment matrix. These accumulated particles appeared to be a similar composition to those collected in the sediment traps, being mostly fine sands.

The depth of the accumulated sediments was broadly similar during winter, spring and summer and, ranged between 0.5–3.0 mm depending on patch size (Fig. 2.8). In contrast, the depth of accumulated sediments in autumn was far lower, between 0–0.6 mm. There was no significant relationship between patch size and the depth of accumulated sediment during autumn, winter or summer. During spring however, the depth of accumulated sediments decreased significantly with patch size (Table 2.2). The three smallest patches in particular, had a greater depth of sediments compared to the other patches (Fig. 2.8c). There was a similar trend, albeit non-significant, for sediment accumulation to decrease with patch size during winter and summer. The variance of sediment accumulation in each patch decreased significantly with patch size (Table 2.3). The three smallest patches in particularly had highly variable levels of sediment accumulation (Fig. 2.4e).

Multivariate description of sub-canopy abiotic environment

PCA of the variance of each abiotic factor (Fig. 2.9a) explained 71% of dataset variability along components 1 and 2. Patches 2 and 3 – and to a lesser extent 1 and 4 – grouped together along component 1, characterised by high variance in relative sub-canopy irradiance and sediment accumulation. PCA of seasonal datasets explained between 66–88% of variability along components 1 and 2. The autumn dataset had patches 1, 2 and 3 grouped together along component 1 (Fig. 2.9b), characterised by high relative sub-canopy irradiance and relative sub-canopy water flow. The remaining patches grouped together centrally except for patches 4, 6 and 7 which were arranged along a gradient of sediment deposition and scour. From winter, patches 1, 2 and 4 (and to a lesser extent 3) were characterised by high relative sub-canopy irradiance and greater depth of accumulated sediments compared to other patches (Fig. 2.9c). However, patches 1 and 2 were separated from 3 and 4 by having higher relative sub-canopy water flow and lower rates of sediment deposition. From spring, patches 1, 2 and 3 were clustered together and characterised by high levels of relative sub-canopy irradiance, relative sediment deposition and sediment accumulation (Fig. 2.9d). The remaining patches were classified along a gradient of relative sub-canopy water flow, except for patches 7 and 10, which were classified based on low sediment accumulation and relative sub-canopy irradiance. Finally, PCA of the summer dataset illustrated patches 1, 2 and 3 as clustered separately and characterised by high relative sub-canopy water flow and sediment accumulation (Fig. 2.9e). Patches 4, 5, 7 and 10 were classified along a gradient of relative sub-canopy water flow and scour, with patches 6 and 9 clustered centrally.

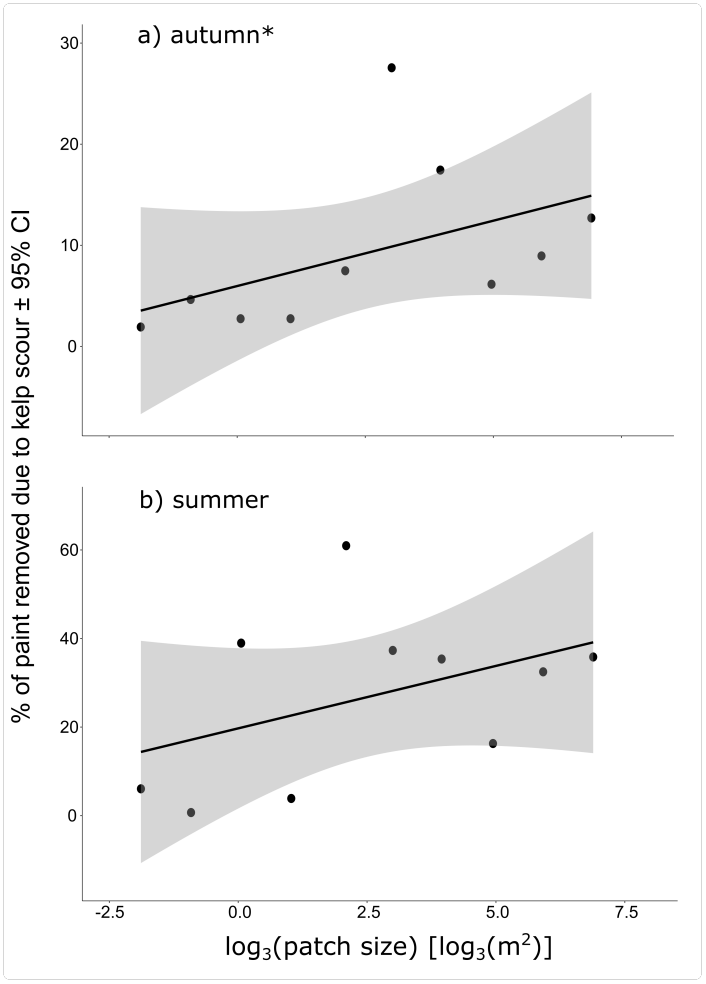

Figure 2.5 Effects of *Ecklonia radiata* patch size on scouring of painted tiles (attached to the substratum) by kelp laminae. Data are mean percentage paint loss. Measurements were recorded over ~72 hours during (a) autumn and (b) summer at a depth of 14 m on reefs in Fortescue Bay, Tasmania, Australia. Note the different y-axis scales. Seasons with significant relationships ($P < 0.05$) are denoted with an asterisk.

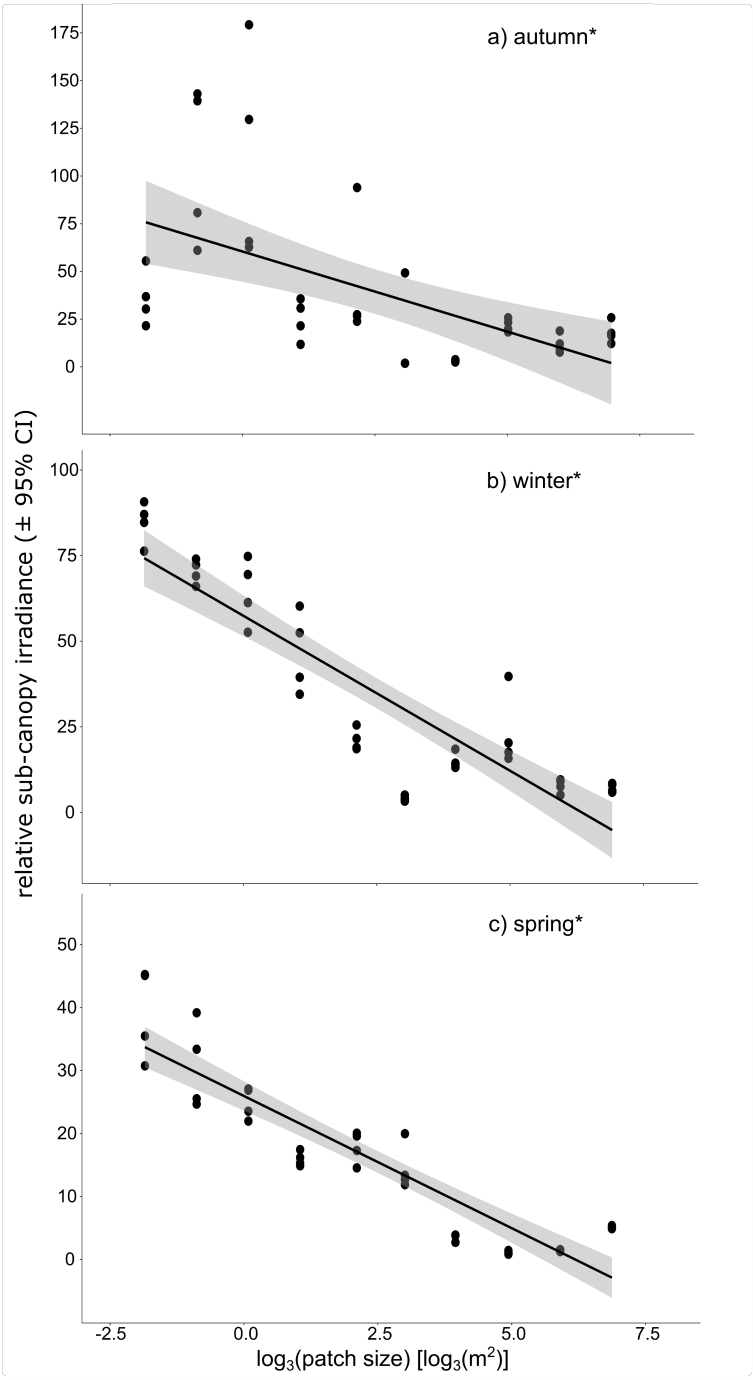

Figure 2.6 Effects of *Ecklonia radiata* patch size on sub-canopy irradiance levels relative to a paired above-canopy measurement. Thus 100% represents equal light below and above the kelp canopy, and values higher or lower than 100% indicate greater or less light below the canopy, respectively. Measurements were taken during three seasons (a–c) at a depth of 14 m on reefs in Fortescue Bay, Tasmania, Australia. Mean (n = 40, ± SE) ambient irradiance during each seasonal sampling period was: autumn 235 ± 14; winter 98 ± 4; and spring 153 ± 4 μmol photon m^{-2} s^{-1}. Note the different y-axis scales. Seasons with significant relationships ($P < 0.05$) are denoted with an asterisk.

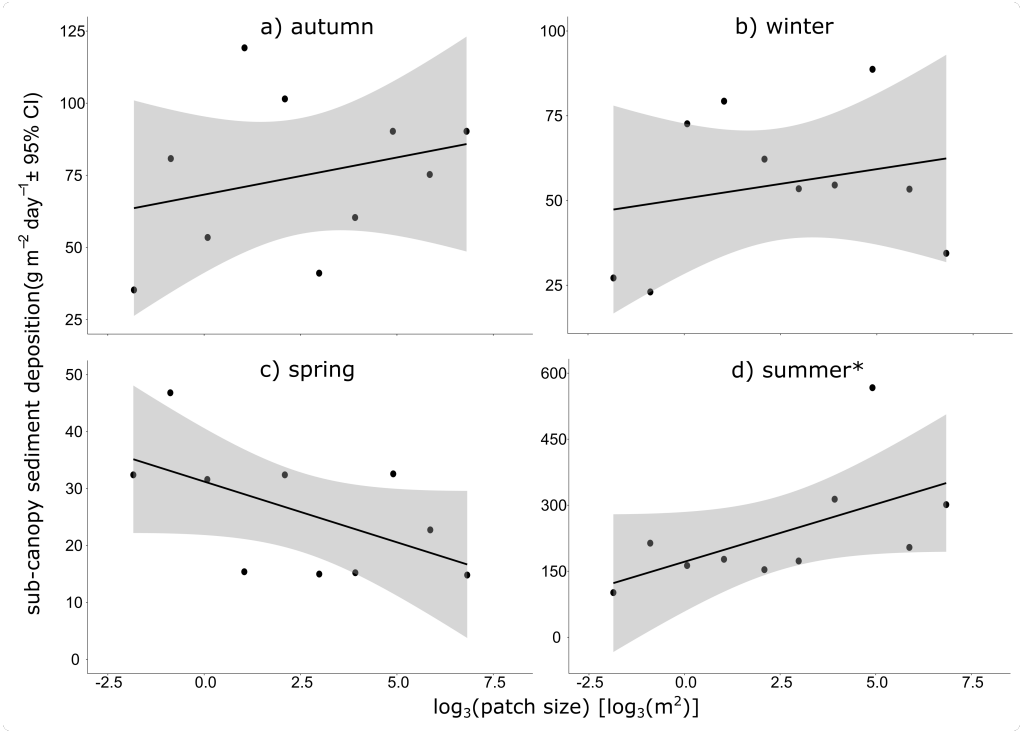

Figure 2.7 Effects of *Ecklonia radiata* patch size on rates of sub-canopy sediment deposition. Measurements were taken during four seasons (a–d) at a depth of 14 m on reefs in Fortescue Bay, Tasmania, Australia. Note the different y-axis scales. Seasons with significant relationships ($P < 0.05$) are denoted with an asterisk.

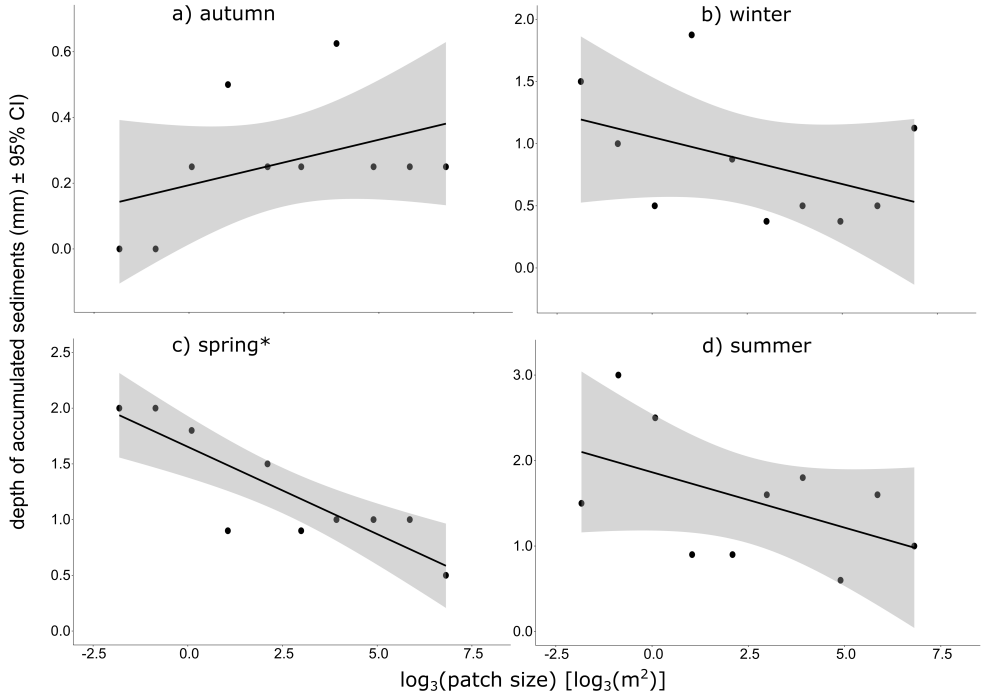

Figure 2.8 Effects of *Ecklonia radiata* patch size on the depth of accumulated sediments entrained within algal turfs growing on the substratum. Measurements were taken across four seasons (a–d) at a depth of 14 m on reefs in Fortescue Bay, Tasmania, Australia. Note the different y-axis scales. Seasons with significant relationships ($P < 0.05$) are denoted with an asterisk.

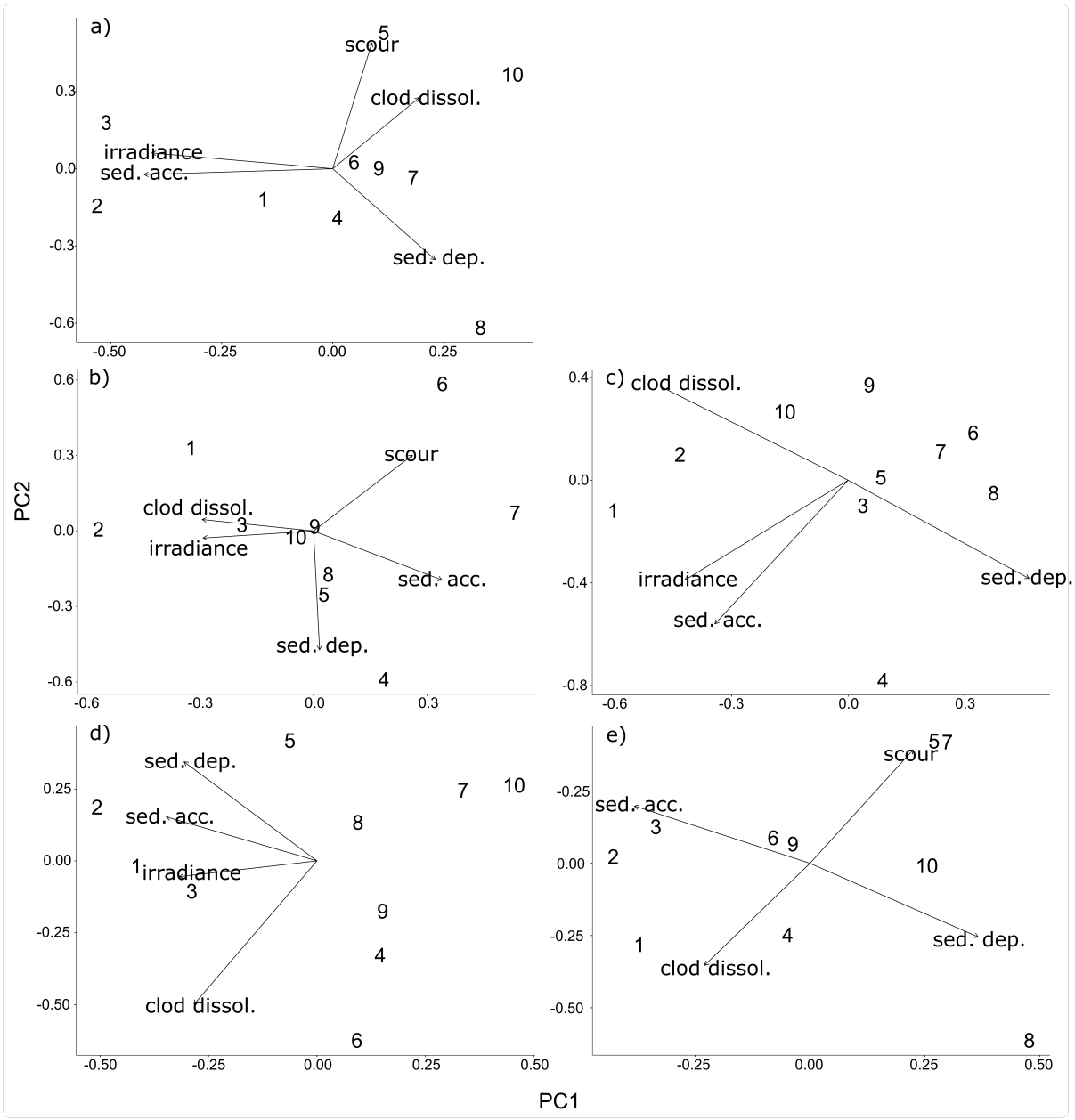

Figure 2.9 Principle Component Analysis (PCA) of abiotic factors within the sub-canopy of ten different sized patches of *Ecklonia radiata* at a depth of 14 m on reefs in Fortescue Bay, Tasmania, Australia. Patch sizes are labelled 1–10 from smallest to largest (see Table 2.1). PCAs are of the (a) overall variance of the abiotic factors and across (b) autumn, (c) winter, (d) spring and (e) summer. Sub-canopy abiotic factors are scour, irradiance relative to above-canopy conditions, clod card dissolution (i.e. water flow) relative to above-canopy conditions, sediment deposition and sediment accumulation.

Discussion

We demonstrate that the physical conditions beneath the *Ecklonia radiata* canopy depend on patch size. While effects differed in magnitude and varied throughout the year, the overall pattern is that reductions in patch size result in increased sub-canopy irradiance, sediment accumulation and water flow, and decreased sediment deposition and kelp scour. The sub-canopy environments of patches <1 m^2 are also more variable compared to larger patches, particularly with respect to light and sedimentation. PCA captured much of the variability from the data and supports the results, frequently clustering the smallest patches together. Since the physical environment is a strong predictor of sub-canopy assemblage structure in *E. radiata* habitats (Kendrick et al. 1999; Irving & Connell 2006a; Toohey 2007) it is likely that reductions in patch size will alter the composition of sub-canopy communities, which may also have broader consequences for juvenile kelp within the sub-canopy.

Abiotic conditions within the sub-canopy

Water flow

Water flow interacts with almost every physiological and physical factor in macroalgae habitats, including nutrient uptake, growth, propagule settlement and dispersal, sub-canopy irradiance (e.g. light-flecking), sedimentation and scour (reviewed by Hurd 2000). Consequently, even subtle alterations to sub-canopy flow may have unexpected, synergistic and far-reaching implications on a suite of processes.

Relative sub-canopy water flow was highly variable, but we detected significant effects of patch size during spring. Canopies of stipitate kelp are effective at interrupting the vertical movement of water (Eckman et al. 1989), meaning that most flow within the *E. radiata* sub-canopy must come through the open sides of patches. Once within the sub-canopy, it is likely water flow is reduced by baffling from the stipes and laminae of *E. radiata,* in conjunction with friction of the water mass along the benthos and underside of the canopy (Fonseca & Fisher 1986; Eckman et al. 1989). This possibly explains why smaller patches of kelp are less effective at moderating ambient flows relative to larger patches; they not only have fewer kelp to baffle and intercept flow, but also a greater ratio of edge to interior from which water enters the sub-canopy.

The role of kelp structure in reducing flow may also explain the seasonal trends we observed. The canopy biomass of *E. radiata* varies throughout the year due to seasonal fluctuations in lamina growth and erosion and is typically highest in spring and summer and lowest during autumn and winter (Larkum 1986; Fairhead & Cheshire 2004). A higher biomass and thicker canopy may explain why we detected strong patch-size effects during spring, and to a lesser extent summer (when trends were evident but non-significant). The lowest relative sub-canopy flow we recorded was also during spring, when flow within the largest *E. radiata* patch was only 45% of ambient conditions. This is

comparable with previous measurements of relative flows beneath a stipitate kelp canopy (comprising a mix of *Agarum* and *Laminaria* kelp species), being 42–50% of above-canopy conditions (Eckman et al. 1989). Low canopy biomass also supports the weaker and more variable modifications of flow observed during autumn and winter. While it is unclear what caused the unusual quadratic curvilinearity in the relationship between flow and patch size in these seasons (Figs. 2.3a, b), we suspect it may be chance natural variability in flow across the site.

Certainly, sea conditions at the site were highly temporally variable and punctuated by extreme episodes (Fig. 2.2). Relative differences in ambient flow between seasons, assessed using above-canopy clod cards, were in general agreement with the modelled wave energy indices from the site, and both methods identified that summer and spring sampling-periods had the highest and lowest ambient conditions, respectively. It is less likely however that our short-term clod card measurements were representative of broader seasonal trends. In particular, clod card installation in winter occurred during a period of unusually mild conditions for that season (Fig. 2.2).

Previous work that has examined how water flow influences *E. radiata* communities has mostly examined broad-scale dynamics, for example exposed versus sheltered reefs (Phillips et al. 1997) or differences across depths (Toohey 2007). Surprisingly, these factors typically explain less of the variation in shallow macroalgae communities than other physical processes (e.g. topography, irradiance) (Phillips et al. 1997; Toohey 2007; Smale et al. 2011). Nonetheless, work has illustrated that increased water flow at the benthos may impair settlement and retention of macroalgae propagules within the sub-canopy (Eckman et al. 1989; Serrão et al. 1996; Graham 2003). Moreover, increased benthic flow can exacerbate negative effects of other abiotic stressors, such as accelerating erosion of the necrotic tissue caused by high light stress in juvenile *E. radiata* (Eckman et al. 1989; Toohey & Kendrick 2007) or increasing the damage and smothering of kelp propagules caused by sediments (Devinny & Volse 1978).

We present some of the first quantitative demonstrations of how *E. radiata* canopies modify sub-canopy flow (see also Wernberg et al. 2005; Irving & Connell 2006a). We recognise that our methodology is unlikely to detect any subtle effects that reductions in patch size may have on sub-canopy flow, especially on deeper reefs less affected by swell. The use of improved technology (e.g. high resolution Acoustic Doppler Velocimeters) is necessary to better characterise the effects of patch size of sub-canopy flow and to discern differences in flow dynamics (e.g. turbulent *vs.* laminar; see Eckman et al. 1989; Hurd 2000) that cannot be resolved using clod cards (Porter et al. 2000).

Scour

During autumn kelp scour increased significantly with patch size, with a similar but non-significant trend in summer. Overall rates of scour were also greater in summer than autumn, which may have been due to higher ambient water flow during summer (Figs. 2.2, 2.3). Overall, during both

autumn and summer, there was very little scour in the four smallest patches (<3 m^2). Scour may be limited in small patches because the inflexible kelp stipe restricts the ability of individuals to scour the benthos at their base (Velimirov & Griffiths 1979; Konar & Estes 2003). This area therefore must be scoured by neighbouring kelp, of which there are fewer in smaller patches. We expect however that rates of kelp scour likely asymptote at relatively small patch sizes (i.e. >3 m^2), and instead becomes a function of kelp density.

Early work demonstrated that kelp scour increases with the density of adult *E. radiata* (Fletcher & Day 1983) and, that kelp with stipes longer than 200 mm cause little scour (Kennelly 1989). However, it is still unclear how generally this applies across different spatial and temporal scales. We have certainly witnessed *E. radiata* with stipes >200 mm scouring the benthos in the experimental patches and elsewhere. Furthermore, beneath canopies of *E. radiata* in Tasmania the highest rates of scour have been detected in areas of intermediate kelp density, with scour declining as kelp density increases or decreases from 3–5 kelp m^{-2} (Tatsumi et al. in prep). It seems that scour is a complex and variable force across both space and time (Figs. 2.4b, 2.5), and is likely affected by local bathymetry, water flow and kelp morphology (Velimirov & Griffiths 1979; Kennelly 1989; Irving & Connell 2006b).

What is known, is that scour is a powerful physical process within *E. radiata* communities where abrasion can inhibit cover of benthic and epifaunal invertebrates (although the response is often species-specific, Fletcher & Day 1983; Kennelly 1989; Connell 2003). Scour also inhibits formation of filamentous turf algae beneath canopies of *E. radiata* (Irving & Connell 2006b), and therefore reduces accumulation of the sediments that get trapped within the turfs (Kennelly 1989; Airoldi 2003). Moreover, the sweeping of the kelp lamina directly removes unconsolidated sediment particles from the benthos (Kennelly 1989). While the removal of sub-canopy sediments likely benefits *E. radiata* (Kennelly 1987a; Airoldi 2003; Strain et al. 2014), abrasion caused by scour may also negatively affect kelp propagules (Dayton et al. 1984).

Consequently, a lessening of kelp scour caused by reductions in *E. radiata* patch size has potential to alter composition of the sub-canopy community by altering the balance between its positive (e.g. sediment removal) and negative (e.g. abrasion) effects (see Connell 2003, 2005). Reduced scour in small patches of *E. radiata* would also result in increases in turf algae and accumulated sediments, as we observed. This is concerning given the well-documented negative effects that turf algae-sediment matrices have on the settlement and recruitment of *E. radiata* and other canopy-forming macroalgae (Kennelly 1987a; Valentine & Johnson 2005; Strain et al. 2014). Conversely, kelp propagules in small patches may benefit from reductions in abrasion, which may counteract the negative effects from turfs and sediments.

Irradiance

We demonstrate that sub-canopy irradiance significantly decreases with increasing patch size of *E. radiata.* This occurred consistently during the three seasons examined (data were not collected in summer due to equipment malfunction). Elevated sub-canopy irradiance was especially noticeable in the three smallest patches (<1 m^2) where it was ~3–6 times higher than in larger patches (Fig. 2.6). Smaller patches have less distance between the centre and edge of the patch, and a greater ratio of edge to interior, therefore more of the incidental irradiance that enters through the open sides of the canopy must reach the interior of smaller patches. Whilst above-canopy irradiance significantly increased with patch size during autumn and winter, we interpret this as a spurious pattern arising from the chance timing of sampling.

Seasonal differences in *E. radiata* canopy biomass likely contributed to the variations we observed in the magnitude of light reduction in the sub-canopy – modification of ambient irradiance by the canopy was greatest during spring (Fig. 2.6), when the canopy is at or near its thickest (Larkum 1986; Fairhead & Cheshire 2004). During spring, sub-canopy irradiance in all patches was never greater than 50% of ambient levels. Whilst the lowest measurement of sub-canopy irradiance also occurred during spring and was ~1% of ambient light or ~1.7 μmol photon m^{-2} sec^{-1}. During autumn – when canopy biomass is relatively low – relative sub-canopy irradiance was notably variable (Fig. 2.6a). This was likely due by short-term variations in ambient irradiance caused by waves, cloud cover or swaying of the canopy, which would disproportionately affect smaller patches due to their reduced canopies and greater ratio of edge to interior (Wood 1987; Toohey & Kendrick 2008). Indeed, smaller patches did have more variable light regimes (Fig. 2.4c).

Overall, the minimum irradiance recorded each season (which always occurred in a different patch) ranged between 1–4% of ambient light, or ~1.7–7.5 μmol photon m^{-2} sec^{-1}. These values are lower than previously reported from beneath *E. radiata* canopies (7–10 μmol photon m^{-2} sec^{-1}, Kennelly 1989; Wernberg et al. 2005). This likely reflects the fact these previous studies were conducted at shallower depths (4–7 m) than our work (14 m). Certainly, stress from increased irradiance on deeper reefs may be more subtle or prolonged due to lower light levels (Wood 1987).

The reduced capacity of the *E. radiata* canopy to modify ambient light conditions in small patches may influence the survival of juvenile kelp in those environments. We observed levels of absolute irradiance within the smaller patches high enough to impair settlement and development of microscopic life stages of kelp (Cie & Edwards 2008). Likewise, macroscopic juvenile sporophytes of *E. radiata* and *E. cava* experience photoinhibition, tissue necrosis and reduced survival and growth when exposed to elevated irradiances (Wood 1987; Altamirano et al. 2004; Toohey & Kendrick 2007). Although, photoacclimation and phenotypic plasticity may enable juvenile kelp that develop

within brighter environment (such as the sub-canopies in small patches) to be more tolerant of increased irradiance (Toohey et al. 2004; Toohey & Kendrick 2007).

Increased sub-canopy irradiance may also influence broader community dynamics. Typically, canopy removal and the consequent increases in light to the benthos results in declines in invertebrates, and corallines and other red algae (Kennelly 1989, Irving & Connell 2006a), and increases in biomass and diversity of foliose and turf algae (Toohey et al. 2004; Wernberg et al. 2005; Flukes et al. 2014). Turf algae, and in particular the sediments it captures, is well recognised to inhibit the recruitment of *E. radiata* and other macroalgae (Kennelly 1987a; Valentine & Johnson 2005; Strain et al. 2014). So, while increased sub-canopy irradiance may increase the diversity and biomass of understorey algae (see also Flukes et al. 2014), it may also delay canopy recovery by suppressing reestablishment of *E. radiata*. The broader implications of this are discussed below.

Sedimentation

Sedimentation involves the separate processes of deposition and accumulation (Airoldi 2003; Connell 2003). Above-canopy sediment deposition rates varied ten-fold throughout the year, which we suspect was due to fluctuations in the amount of suspended sediments due to seasonal changes in sea conditions (Komar & Miller 1973, Fig. 2.2). There are no other major nearby sources of sediments (i.e. large rivers), and sediments characteristics (e.g. colour, composition) did not appear to vary throughout the year.

Sediment loads were greatest in summer, which was also the season when significant effects of patch size were present, with larger patches experiencing higher rates of deposition. This was likely due to greater baffling of sub-canopy flow in larger patches, leading to increased settling of sediment particles from the slowed water mass (Komar & Miller 1973; Fonseca & Fisher 1986; Eckman et al. 1989). It is unclear why the measures of sediment deposition do not precisely correlate with the patterns of relative sub-canopy water flow during summer. Differences in timing of sampling, or in the magnitude of flow that significantly affects clod card dissolution versus suspension and settling of sediment particles may explain this disparity (Komar & Miller 1973; Jürg 1996; Porter et al. 2000).

Our results demonstrate the sensitivity of particle deposition rates to patch size – presumably because of differences in sub-canopy hydrodynamics. This effect is likely extended to other small particles such as larvae and propagules (Eckman et al. 1989; Serrão et al. 1996) and has clear implications for settlement and dispersal of kelp and other organisms. Thus, reductions in patch size might result in fewer opportunities for larvae or propagules to be deposited and/or retained within the sub-canopy of kelp patches (Eckman et al. 1989; Graham 2003; Smale et al. 2011).

The accumulation of sediment was significantly affected by patch size during spring, when greater amounts accumulated in smaller patches. There were also similar, but non-significant, trends

during winter and summer. Distinctly higher and more variable levels of sediment accumulation in the three smallest patches (Figs. 2.4, 2.8) indicates the possibility of a threshold patch size below which sediment accumulation in *E. radiata* patches is exacerbated, which in turn may be linked to levels of sub-canopy light and scour.

One of the defining features of the sub-canopy environment within intact *E. radiata* stands is the near-absence of accumulated sediments (Kennelly 1987a; Airoldi 2003; Connell 2003). Our results demonstrate that sediment accumulation in *E. radiata* habitats is not linked to sediment deposition rates, which typically had the reverse trend of being greater in larger patches. Moreover, dramatic seasonal differences in the rates of deposition did not manifest as seasonal differences in sediment accumulation (c.f. spring vs summer, Figs. 2.4c, d & 2.5c, d). Sediment accumulation therefore seems decoupled from sediment deposition; manifested by the sweeping of kelp that clears loose sediments (Kennelly 1989), the combination of low light/high scour that prevents extensive turf algae cover beneath established *E. radiata* canopies (Irving & Connell 2006a), and proliferation of the sediment-trapping turf algae where *E. radiata* is sparse or absent (Irving & Connell 2006b). Thus, creating the widespread pattern that on semi-exposed coastal reefs, sediment accumulation correlates positively with sub-canopy irradiance and negatively with scour because increasing irradiance and decreasing scour promote the cover of turf algae (Kennelly 1987b; Connell 2005). These interrelationships between scour, irradiance and sediment accumulation are evident in our results (Figs. 2.5, 2.6, 2.8).

The negative effects of sediments on *E. radiata* and the associated community are well documented (Kennelly 1987a; Airoldi 2003; Strain et al. 2014). Sediment inhibits the presence and persistence of algae and sessile invertebrates on the benthos due to smothering, abrasion and substrata instability (Fletcher & Day 1983; Irving & Connell 2006a). As mentioned earlier, sediments and turf algae also inhibit the settlement and recruitment of *E. radiata* (Kennelly 1987a; Valentine & Johnson 2005). While the specific mechanisms remain to be tested for *E. radiata*, even small amounts of sediment (<50 mg^{-1} cm^{-2}) can inhibit the attachment and development of the propagules of other kelp species (Devinny & Volse 1978; Watanabe et al. 2016). The negative effects of sediments on macroalgae are also intensified by smaller sediment particle sizes (<599 μm) and increased benthic flow (Devinny & Volse 1978; Watanabe et al. 2016) – two factors that are applicable to our observations.

Multivariate characterisation of the sub-canopy environment

PCA allowed us to explore which parameters were most important in characterising variability in the sub-canopy environment of our *E. radiata* patches. PCA typically captured a large proportion of dataset variability (>70 %), and the three or four smallest patches of *E. radiata* were consistently clustered together based on the characteristics of their sub-canopy environment (Fig. 2.9).

It was sub-canopy irradiance and sediment accumulation that most consistently differentiated these small patches from larger ones, supporting the univariate patterns we observed.

Ecological implications and consequences of reductions in patch size

We have demonstrated that smaller patch sizes reduce the capacity of *E. radiata* to engineer and modify the local abiotic environment beneath the kelp canopy. Ecosystem engineering by macroalgae is one of the dominant forces shaping temperate subtidal reef communities (Dayton et al. 1984; Wernberg et al. 2005; Steneck & Johnson 2014). In fact, the presence and composition of macroalgae canopies in Australia can be used to reliably predict the assembly of the sub-canopy community (see Irving & Connell 2006a) – and there are consistent associations between intact *E. radiata* canopies and encrusting and red algae, and between canopy-gaps and foliose of turf algae (Kennelly 1987b; Kendrick et al. 1999; Toohey et al. 2004; Irving & Connell 2006a). It follows, that reductions in the capacity of *E. radiata* to engineer abiotic change will weaken these effects, so that habitat fragmentation may result in understorey communities becoming more characteristic of gap communities. While gaps within intact kelp canopies can facilitate biodiversity (Irving & Connell 2006a), a shift in the sub-canopy environment to become more gap-like could lead to overall reductions in habitat structure and heterogeneity. Experiments have already shown that reductions in *E. radiata* density – which like fragmentation is another manifestation of habitat degradation – precipitate this response (Flukes et al. 2014).

The diminished capacity of *E. radiata* to act as an ecosystem engineer may also feedback to affect the kelp itself. This is especially so for the juvenile life stages that settle and develop within the sub-canopy, and which may benefit from stress amelioration (i.e. high light and sedimentation) as a form of intraspecific facilitation from adult conspecifics (Bennett & Wernberg 2014). Certainly, existing work has demonstrated the potential for feedbacks to occur between the engineer and the engineered local environment (Wernberg et al. 2005; Cuddington et al. 2009; Jones et al. 2010).

To this end, the most far-reaching consequence of fragmentation of *E. radiata* habitats may be a reduction in ecosystem resilience. The turf assemblages that look set to increase due to reductions in patch size seem very likely to inhibit the settlement and recruitment of juvenile *E. radiata* (Kennelly 1987a; Valentine & Johnson 2005; Gorman & Connell 2009). Thus, it follows that a fragmented *E. radiata* habitat with reduced recruitment of juveniles would be at increased risk of further degeneration and phase shift from the structurally complex and biodiverse kelp habitat to a simpler and less diverse turf algae habitat (Strain et al. 2014). Phase shifts of this form have already been observed in Australia (Valentine & Johnson 2005; Gorman & Connell 2009) and elsewhere (Strain et al. 2014; Krumhansl et al. 2016), and have an array of flow-on effects that include a reduction in ecosystem productivity and the restructuring of trophic provisioning and food webs (Johnson & Mann 1988; Falkenberg et al. 2015). Of further concern, is that ocean warming and

acidification may increase the cover and persistence of turf algae (Falkenberg et al. 2015) and also impair the growth of juvenile *E. radiata* (Britton et al. 2016), further eroding kelp forest resilience.

Conclusion

We present some of the first experimental manipulations of *E. radiata* on reefs deeper than 12 m, where fundamental abiotic conditions (e.g. light, hydrodynamics) are markedly different to shallower reef habitats. We conclude that fragmentation of *E. radiata* habitats is likely to alter local physical conditions and may cascade to influence composition of the sub-canopy and kelp forest resilience. The magnitude of the effects may differ across seasons or locations, but small patches of *E. radiata* seem likely to experience increased sub-canopy irradiance, sedimentation and water flow, and decreased kelp scour. The capacity of adult *E. radiata* to engineer abiotic change is impaired in small patches due to both fewer individuals, and a greater influence of the patch edge on the sub-canopy environment. Crucially, these novel abiotic conditions are likely to alter sub-canopy community composition towards a state that is less suitable to juvenile *E. radiata* and may therefore influence the persistence of this important ecosystem engineer and the associated community.

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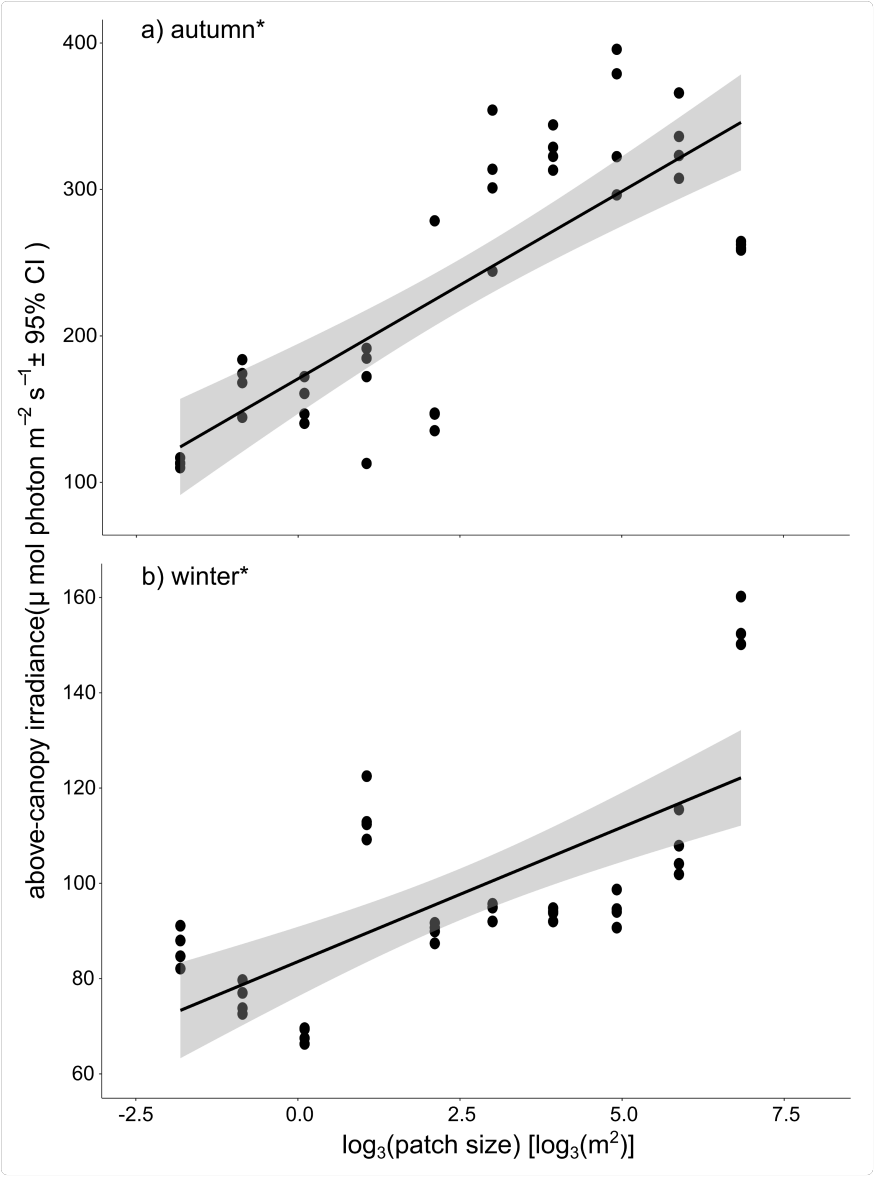
Appendices

Appendix 2.1 Output from linear regressions examining how above-canopy abiotic conditions vary with patch size within seasons. Response variable and associated transformation is noted in the first column. The factor, patch size, was $\log_3$-transformed to best meet test assumptions. Significant relationships denoted in bold and with an asterisk.

data analysed	*F-value*	*P-value*
WATER FLOW		
autumn $(Y)^{-1.60}$	$F_{(1,8)} = 0.002$	0.962
winter $(Y)^{-3.50}$	$F_{(1,8)} = 0.005$	0.945
spring $(Y)^{1.50}$	$F_{(1,8)} < 0.001$	0.984
summer $(Y)^{6.00}$	$F_{(1,8)} = 1.947$	0.200
IRRADIANCE		
autumn $(Y)^{0.15}$	$F_{(1,38)} = 75.25$	**<0.001***
winter $(Y)^{-1.00}$	$F_{(1,38)} = 37.34$	**<0.001***
spring $(Y)^{-1.00}$	$F_{(1,38)} = 0.071$	0.791
SEDIMENT DEPOSITION		
autumn $(Y)^{-0.40}$	$F_{(1,8)} = 0.053$	0.823
winter $(Y)^{0.50}$	$F_{(1,8)} = 0.673$	0.436
spring $(Y)^{0.40}$	$F_{(1,8)} = 0.017$	0.901
summer $(Y)^{-0.50}$	$F_{(1,8)} = 0.501$	0.499



Appendix 2.2 Significant relationships between *Ecklonia radiata* patch size and above-canopy (i.e. ambient) irradiance. Measurements were taken during (a) autumn and (b) winter at a depth of 14 m on reefs in Fortescue Bay, Tasmania, Australia. In (a) irradiance correlates with the time of day that measurements were made, in (b) they reflect patterns of cloud cover. Thus, although above-canopy irradiance-patch size relationships are spurious, they indicate the necessity to express sub-canopy irradiance relative to above canopy levels. Note the different y-axis scales. Seasons with significant relationships ($P < 0.05$) are denoted with an asterisk.

Chapter 3. Press perturbation causes collapse of recruitment in a fragmented kelp forest

Cayne Layton, Matthew J. Cameron, Masayuki Tatsumi, Victor Shelamoff, Jeffrey T. Wright and Craig R. Johnson

Abstract

Kelp forests around the world are experiencing disturbances from anthropogenic sources such as ocean warming and overgrazing. Unlike natural disturbances to kelp forests, such as storms, many anthropogenic disturbances manifest as press perturbations with persistent alterations to the environment. One consequence of this degradation is that kelp forests in many regions are becoming increasingly sparse and fragmented. We manipulated patch size of the kelp *Ecklonia radiata* to simulate persistent habitat fragmentation and assessed how patch size influenced the demography of macro- and microscopic juvenile life stages of *E. radiata*. This persistent press disturbance resulted in eventual collapse of juvenile kelp recruitment, but only in patches smaller than 1 m^2. However, this disturbance initially resulted in short-term increase in recruitment in those same patches. Experimental transplants of microscopic and established juvenile sporophytes (> 50 mm) did not identify the life stage impacted by the persistent reductions in patch size, suggesting the effects may be subtle and require extended periods to manifest and/or that another life stage is responsible. The impaired ability of *E. radiata* to engineer abiotic change within small patches seemingly led to the proliferation of turf algae and sediments over time, and ultimately, to the collapse of recruitment of juvenile *E. radiata.* We demonstrate the consequences of short and long-term degradation of *E. radiata* habitats and conclude that habitat fragmentation can cause severe disruptions to the demography of *E. radiata* in smaller patches. This has clear consequences for kelp resilience and recovery in the face of increasing anthropogenic threats.

Introduction

Kelp (Order Laminariales) dominate shallow coastal environments in temperate latitudes around the world (Steneck et al. 2002; Krumhansl et al. 2016). These ecosystem engineers (*sensu* Jones et al. 2010) create spatially complex habitats with sub-canopy environments that support diverse and productive ecosystems (Graham et al. 2007; Teagle et al. 2017). Most natural disturbances within kelp forests can be described as pulse perturbations that cause rapid alterations to species and the habitat (Bender et al. 1984). An important physical disturbance affecting kelp forests are storms and associated wave energy (Kitching 1937; Dayton & Tegner 1984). By removing or thinning the kelp canopy, these disturbances alter sub-canopy conditions and the understorey community (Dayton et al. 1984; Kennelly 1987a) and assist in maintaining local diversity and heterogeneity (Sousa 1984; Dayton et al. 1984, 1992).

Increasingly however, kelp habitats are experiencing disturbances from anthropogenic sources, such as marine heatwaves and overgrazing (Johnson et al. 2011; Krumhansl et al. 2016; Wernberg et al. 2016). Many of these disturbances manifest as press perturbations with persistent alterations to the environment (Bender et al. 1984), such that kelp habitats in many places around the world are becoming increasingly sparse and fragmented (Steneck et al. 2008; Ling et al. 2015; Wernberg et al. 2016).

Habitat fragmentation and reductions in kelp patch size will likely result in increased edge effects and changes to the abiotic conditions (e.g. sub-canopy light and sedimentation) within smaller patches (Dayton et al. 1984; Chapter 2). These effects may be of particular importance if they interrupt internal drivers that support demographic processes, such as intraspecific facilitation via an 'environment-engineer feedback' (Cuddington et al. 2009; Jones et al. 2010). Indeed, this may explain the slow recovery of some kelp species that is often observed after large-scale losses (Dayton et al. 1992; Connell et al. 2008; Angelini & Silliman 2012). It is therefore critical to understand how the degradation of kelp habitats affects their ongoing resilience and recovery (Dayton et al. 1984; Wernberg et al. 2010; Angelini & Silliman 2012). The examination of disturbed kelp habitats may also help illustrate the necessity of human intervention and how best to implement and focus any restoration efforts (see Johnson et al. 2017).

The most widespread and abundant species of kelp in Australasia, *Ecklonia radiata*, is one species suffering declines throughout its range. This stipitate kelp (*sensu* Dayton et al. 1982) rarely grows taller than 1.5 m, but creates dense and complex habitats with levels of productivity that equal or exceed many other kelp species (Larkum 1986; Kirkman 1989). *Ecklonia radiata* is the dominant habitat-forming macroalgae on the Great Southern Reef – Australia's continental-wide temperate reef system – and the foundation of ecosystems with high levels of biodiversity, endemism and economic value (Bennett et al. 2016). However, populations of these species throughout Australia are under

threat from coastal development, ocean warming and overgrazing (Connell et al. 2008; Ling 2008; Vergés et al. 2016; Wernberg et al. 2016).

Marine heatwaves have caused substantial range contractions of *E. radiata* in Western Australia (Wernberg et al. 2016). But despite wholesale mortality in some areas, intraspecific variation in thermal tolerance (Mabin et al. 2013; Mohring et al. 2014) results in the patchy resistance and recovery of *E. radiata,* especially at the margins of warming events (Wernberg et al. 2010). Increasing water temperatures are also leading to overgrazing of *E. radiata* in eastern Australia by range-extending herbivores such as tropical fishes (f. Kyphosidae, Siganidae; Vergés et al. 2016) and the urchin *Centrostephanus rodgersii* (which has also benefitted from overfishing of urchin-predators such as rock lobsters; see Johnson et al. 2011). Damage from overgrazing is not instantaneous however, and kelp habitats are persistently disturbed and fragmented before extirpation occurs (Ling 2008; Flukes et al. 2012; Vergés et al. 2016).

Given the abiotic changes that occur as the patch size of *E. radiata* decreases (e.g. increased light and sedimentation, Chapter 2) we predict demographic rates will be negatively affected by reductions in patch size. To test these predictions, we assessed how persistent reductions in patch size affects the demography of the juvenile life stage of *E. radiata*. We assessed the density of juvenile and adult *E. radiata* across a range of differently sized patches (0.1–2025 m^2), which were maintained for 24 months to simulate the persistent impacts effects of habitat fragmentation caused by anthropogenic stressors. Microscopic and macroscopic juvenile kelp sporophytes were also transplanted into the experimental patches to test how these life stages respond to reductions in patch size. In conjunction with work that characterised the physical environment in these same patches (Chapter 2), we examine direct and indirect effects of reductions in patch size on the demography of juvenile *E. radiata*. Ultimately, we explore how habitat degradation influences the resilience and stability of *E. radiata* habitats, and address knowledge gaps critical to the future management and conservation of kelp forests (Schiel & Foster 2006; Evans et al. 2017)

Methods

Study site

The field site (-43.13735, 147.96819) was located within Fortescue Bay in southeast Tasmania, Australia. The site is semi-exposed and subject to occasional ocean swell, with dolerite reef dominated by *Ecklonia radiata*. In February 2014, ten approximately square patches (0.1, 0.3, 0.9, 2.7, 9, 25, 73, 225, 676 and ~2025 m^2) were established within the largely continuous stand of *E. radiata* at a depth of 14 m. For full details and a map of the experimental patches see Chapter 2, but briefly, patches were created by clearing all canopy-forming algae (i.e. any species with adults >300 mm in height) from a 2 m wide “buffer” around the measured patch perimeter. These buffer areas

were maintained every 6 weeks and any new canopy-forming algae removed. The largest patch did not have a buffer as it was a naturally isolated (by sand) patch reef. Experimental patches were separated from each other by at least 5 m, except in one instance where due to reef bathymetry it was necessary for two patches to have adjoining buffers on one side (i.e. 4 m)

Kelp demographics

Juvenile and adult sporophyte densities

Density assessments were conducted at the start of the experiment (February 2014), and then seasonally (every 12.5 ± 1 weeks, SE) in autumn 2014 (April), winter 2014 (July), spring 2014 (October), summer 2015 (February), autumn 2015 (May), winter 2015 (July), spring 2015 (October) and summer 2016 (January). When assessing the density of *E. radiata* sporophytes, individuals were classed as either juveniles (stage 1) or adult (stages 2 and 3; *sensu* Kirkman 1981). These assessments provided estimates of recruitment (stage 1) and an indication of the proportion of juveniles that matured (stages 2 and 3) in each patch. In the five smallest patches (≤9 m^2) it was possible to census all visible (>5 mm) sporophytes, this was not possible in larger patches, which were instead subsampled by counting all visible sporophytes within five randomly positioned 1 m^2 quadrats. To scale sporophyte density to one metre-square, it was necessary to multiply the counts from the patches smaller than 1 m^2. This resulted in artificially elevated sporophyte abundances in those patches – especially for the two smallest patches – but did not affect overall interpretation of the results.

Growth and survivorship of macroscopic juveniles

It was not possible to tag and follow juveniles due to the large size of many of the patches and the time limitations of using SCUBA at 14 m depth. Instead, we determined the survivorship and growth of juveniles by transplanting stage 1 juveniles into each patch. These stage 1 juveniles (50–150 mm in length) were collected from the intact stand of *E. radiata* surrounding the experimental patches. Each juvenile was measured to the nearest 2 mm and hole-punched at the base (i.e. proximal end) of the lamina above the meristem to determine growth. Ten juvenile sporophytes were then threaded into the twine of nylon rope at 100 mm intervals, and one rope secured in the centre of each experimental patch each time. After 42 ± 1 days (SE), the growth – measured from the top of the holdfast to the base of the punched-hole – of each transplanted sporophyte was measured to the nearest 2 mm *in situ*, and the sporophyte hole-punched again in the original proximal position. If a sporophyte was missing the position was noted and the individual recorded as not surviving. After 90 ± 5 days (SE) the ropes were collected, and growth and survivorship determined again. Pilot studies confirmed that growth measurements were identical regardless of whether they were made *in situ* or *ex situ*. Preliminary analyses revealed growth rates of the juvenile sporophytes (mm/week) were linear and independent of initial sporophyte length. Macroscopic juveniles were outplanted in autumn

(March), winter (June) and spring (September) in 2015 and summer in 2016 (January). The sporophytes transplanted during summer 2016 were only installed for the 42-day period, due to termination of the experiment and destructive sampling of the patches.

Post-recruitment survivorship of microscopic sporophytes

Lab-cultured microscopic sporophytes were outplanted to examine survivorship of the life stage in each patch. Blank microscope slides deployed at the same times measured background natural recruitment of *E. radiata* propagules and acted as controls. Outplanting occurred in spring 2014 and spring 2015. The reproductive tissue for culturing was collected from stage 3 *E. radiata* from the area surrounding the experimental patches, and culturing followed the methods of Mabin et al. (2013) and Tatsumi & Wright (2016). Briefly, zoospores at a density of ~7000 mL^{-1} were settled onto fully-frosted microscope slides submerged in UV-sterilized and filtered (0.2 μm pore-size) seawater, and the culture maintained for 42 days. Following this incubation period, 10 randomly selected slides were assessed under a microscope to ascertain mean sporophyte abundance prior to outplanting, which was ~8050 (± 400, SE) sporophytes $slide^{-1}$. Four randomly selected slides with cultured sporophytes, and four blank fully-frosted microscope slides (which had been curing in filtered seawater during the culturing process) were then attached in random order to a plastic rack. The racks were transported to the experimental site submerged in seawater in an insulated container. At the site, divers secured three racks (i.e. 12 slides supporting sporophytes and 12 control slides) in the approximate centre of each patch. After 49 days (± 3 days, SE) the racks were collected and transported to the lab where all surviving sporophytes on the slides were counted.

Data analysis and statistics

Data were primarily analysed using linear regression of the demographic response variable against patch size. Test assumptions were assessed using diagnostic plots, model residuals and the Shapiro-Wilk normality test. Data that did not meet test assumptions were transformed based on values of λ from Box-Cox plots, which is noted in the model output. The addition of a small constant was required to ensure an appropriate transformation when the response variable was zero and is noted in the model output. Patch size was $\log_3$-transformed prior to testing since patch sizes were initially determined on an approximately $\log_3$ scale (see Table 3.1 for transformed patch sizes). In one instance, data could not be appropriately transformed due to the influence of an outlier. For completeness, we present the full data along with the test based on the data with the outlier excluded.

Table 3.1 Untransformed and transformed values of the size of experimental patches.

patch size (m^2)	log_3(*patch* size) [$log_3(m^2)$]
0.1	-2.10
0.3	-1.10
0.9	-0.10
2.7	0.90
9	2.00
25	2.93
73	3.91
225	4.93
676	5.93
2025	6.93

Data on density of juvenile kelp were often strongly nonlinear, but analyses using Generalized Linear Models and Generalized Additive Models were rejected due to uncaptured curvilinearity and overfitting, respectively. Subsequently, some of these data were analysed using nonlinear regression based on nonlinear least squares. Here we used the same methods as for the linear regressions to ensure test assumptions were met. Nonlinear regression uses an iterative procedure to estimate model parameters based on a user-specified function, which we specified as a negative-power function based on graphical exploration of the data. Each model was re-fitted using different starting values to ensure reliability, but the best fit for each model was always achieved on the first attempt. *P*-values and confidence intervals cannot be robustly calculated for nonlinear regression (Bates & Watts 1988; Quinn & Keough 2002) so we primarily utilise nonlinear regression as a graphical tool. Overall, this approach was used sparingly and only when important curvilinearity in the data was not captured by linear regression. A pseudo-r^2 was calculated for nonlinear regression models from the linearised form of a log-log model (of which a negative-power function is the nonlinear form). Analyses were conducted using the *MASS, lattice* (linear regressions) and *nls* (nonlinear regression) packages in *R* (v. 3.2.5, *R* Core Team), with alpha at $\alpha = 0.05$. Figures are presented with untransformed response variables for clarity and were produced using the *ggplot2* package in *R* along with *Inkscape* (v. 0.91).

Results

Juvenile sporophyte densities

Initial mean density of *Ecklonia radiata* juvenile sporophytes was 1.7 ± 0.28 m^{-2} and did not differ significantly among patches (Table 3.2). In autumn 2014, approximately 8 weeks after the creation of the patches, there was a dramatic increase in the density of juveniles in the four smallest

patches (<3 m^2, Fig. 3.1). Nonlinear regression clearly identified a strong negative power relationship at this time between density of juveniles and patch size (Fig. 3.2a). The density of juvenile sporophytes in most patches continued to increase in winter 2014, and for many patches, including the four smallest, the densities observed at the time were the highest from throughout the study (Fig. 3.1). The highest density of juveniles recorded (~170 juveniles m^{-2}) was in the smallest patch (0.1 m^2). This was amplified somewhat due to scaling to a per metre-square basis, but still indicates the presence of 17 stage 1 sporophytes within this 0.1 m^2 patch. During this time, the relationship between density of juveniles and patch size was again strongly and negatively nonlinear (Fig. 3.2b). In spring 2014, the density of juveniles in most patches declined almost as steeply as it rose. Notably, this was the start of a general decline in the density of juveniles in the smaller patches, of which the three smallest patches never recovered (Fig. 3.1). Nonetheless, there was still an overall pattern of decreasing density of juvenile sporophytes with increasing patch size throughout this period. This relationship was linear and highly significant during spring 2014 (Fig. 3.2c; Table 3.2), and strongly nonlinear (but still negative) during summer 2015 and autumn 2015 (Fig. 3.2d, e).

Approximately 16 months after the beginning of the experiment and between the autumn and winter 2015 samples, the density of juveniles in the three smallest patches declined to zero (Fig. 3.1). For the remaining 8 months, no juvenile sporophytes were detected in any of these patches. In patches larger than 2.7 m^2, there was generally a small increase in density of juveniles between autumn 2015 and winter 2015. Overall, the relationship between density of juveniles and patch size also changed dramatically between autumn and winter 2015, shifting from strongly negative in autumn 2015 to significantly positive in winter 2015 (Fig. 3.2e, f; Table 3.2).

The remaining seasons saw relatively minor changes in the density of juveniles across the patches, but some patches experienced another increase in juveniles throughout spring 2015. Despite minor fluctuations among patches over time (Fig. 3.1), the relationship between density of juveniles and patch size remained strongly and significantly positive (Fig. 3.2, Table 3.2). The final sampling period in summer 2016 saw slight decreases in the density of juveniles in most patches from the previous seasons (Fig. 3.1), although there was still substantial recruitment in the 2.7 m^2 patch (the outlier in Fig. 3.2h). Excluding the outlier, the relationship with patch size was significant and positive as in the previous two seasons (Fig. 3.2h, Table 3.2).

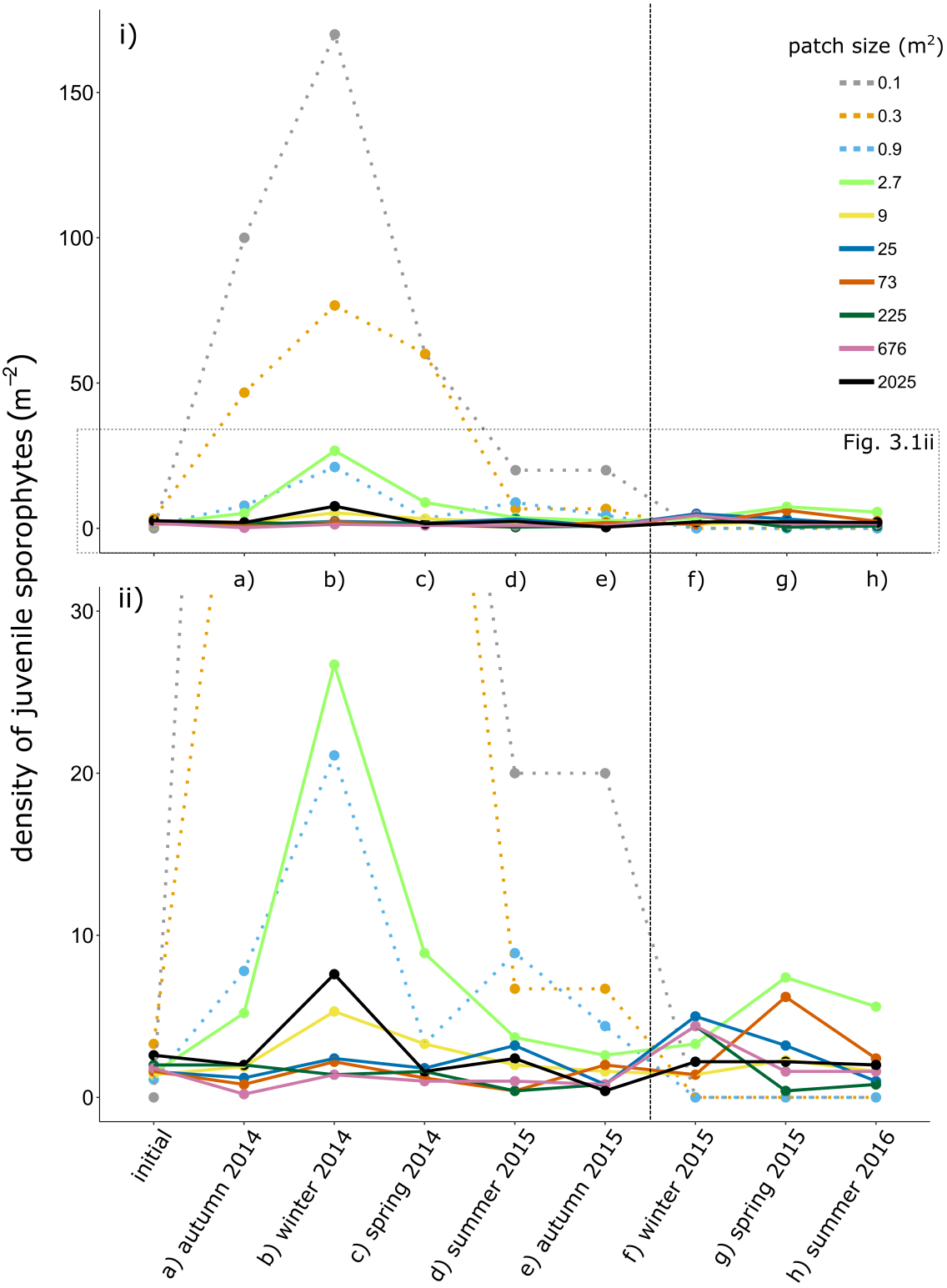


Figure 3.1 Time-series of juvenile *Ecklonia radiata* sporophyte density over 24 months within 10 different patch sizes. Season notation (a–h) matches Fig. 3.2a–h. Upper facet (i) is full data and (ii) lower facet is an expanded version with the y-axis scale adjusted for clarity. The three smallest patches that experienced an eventual collapse in recruitment have dashed lines, and the remaining patches have solid lines. The vertical dotted line indicates the time when juvenile kelp were no longer present in the three smallest patches.

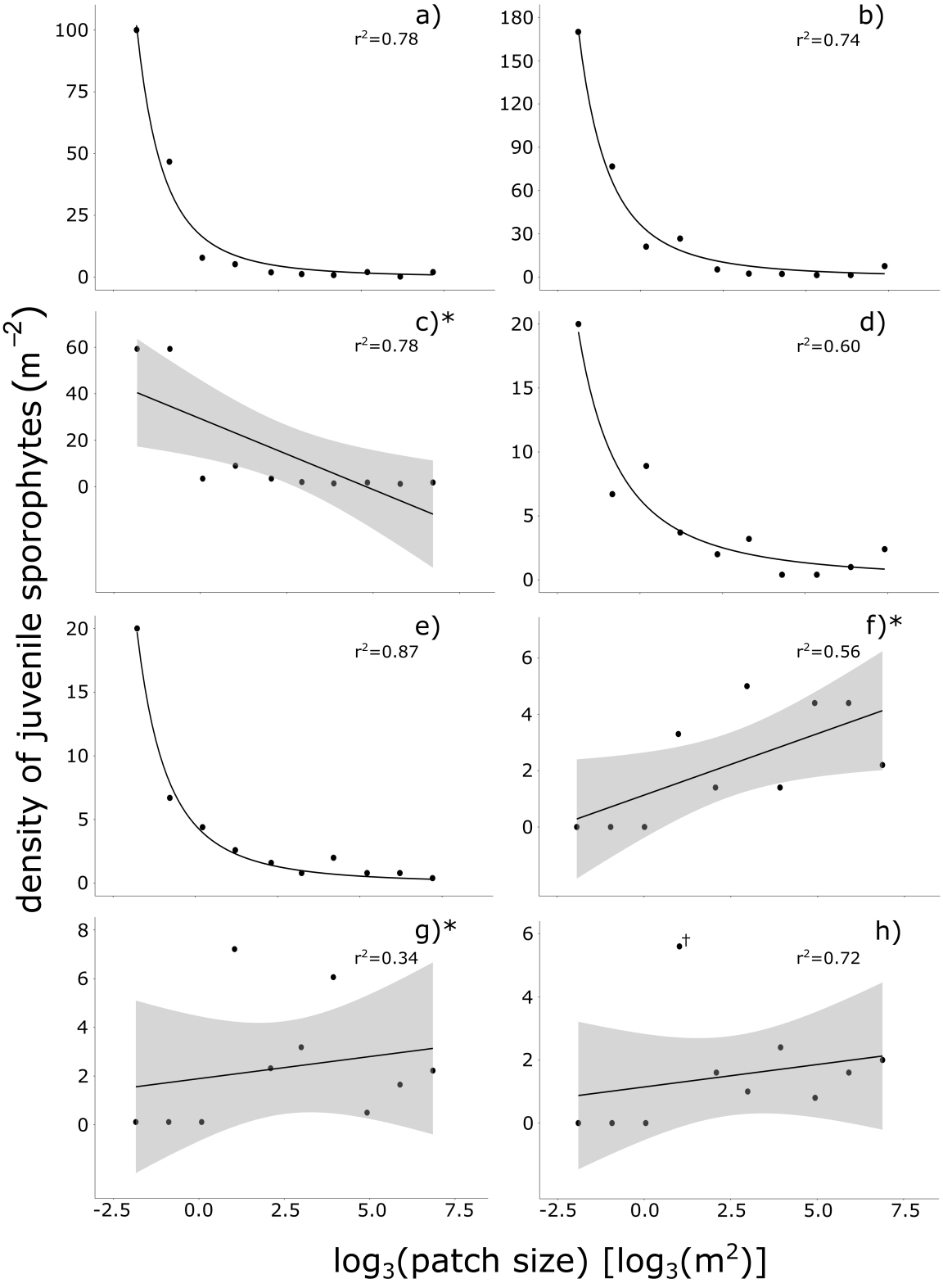


Figure 3.2 Nonlinear and linear regression of relationship between juvenile *Ecklonia radiata* sporophyte and patch size over 8 seasons. Season notation (a–h) matches Fig. 3.1. Linear regression plots (c, f–h) have 95% CI (grey shading); see Methods for details. Significant non-zero slopes ($P < 0.05$) for linear regression tests are denoted with an asterisk. Nonlinear regressions were unable to be significance tested. The cross on panel (h) denotes the outlier that when removed resulted in a significant relationship (see Table 3.2).

Table 3.2 Regression of relationship between juvenile *Ecklonia radiata* sporophyte density and patch size over 8 seasons. Response variable and associated transformation is noted in the first column. The factor, patch size, was $\log_3$-transformed to best meet test assumptions. Season notation (a–h) matches Figs 3.1 and 3.2. The symbol § indicates a nonlinear relationship that was unable to be tested for significance (see Methods for details). Significant relationships for linear regression tests denoted in bold and with an asterisk. The † denotes the model where an outlier barred testing, the outlier-excluded data (presented) were retested for completeness.

data analysed	*F-value*	*P-value*
initial $(Y+0.01)^{0.75}$	$F_{(1,8)} = 1.946$	0.201
a) autumn 2014§	n/a	
b) winter 2014§	n/a	
c) spring 2014 $(Y)^{-0.55}$	$F_{(1,8)} = 32.62$	**<0.001***
d) summer 2015§	n/a	
e) autumn 2015§	n/a	
f) winter 2015 $(Y + 0.01)^{0.3}$	$F_{(1,8)} = 12.592$	**0.008***
g) spring 2015 $(Y + 0.01)^{0.1}$	$F_{(1,8)} = 5.601$	**0.045***
h) summer 2016† $(Y + 0.01)^{0.25}$	$F_{(1,7)} = 21.89$	**0.002***

Table 3.3 Linear regression of survivorship and growth of transplanted macroscopic juvenile *Ecklonia radiata* sporophytes against patch size. Assessments were taken at ~42 and ~90 days after transplanting for each season, and data also pooled to produce total annual survivorship. Response variable and associated transformation is noted in the first column. The factor, patch size, was $\log_3$-transformed to best meet test assumptions. During summer 2016, juvenile sporophytes were only installed for ~42 days. Significant relationships denoted in bold and with an asterisk.

data analysed	*F-value*	*P-value*
SURVIVORSHIP OF TRANSPLANTED JUVENILE SPOROPHYTES		
total survivorship annually @ 42 days $(Y)^{5.5}$	$F_{(1,8)} = 1.191$	0.307
total survivorship annually @ 90 days $(Y)^{-1.25}$	$F_{(1,8)} = 1.950$	0.200
autumn 2015 @ 42 days $(Y)^{1.4}$	$F_{(1,8)} = 0.534$	0.485
autumn 2015 @ 90 days	$F_{(1,8)} = 0.164$	0.696
winter 2015 @ 42 days $(Y)^{4.5}$	$F_{(1,8)} = 0.295$	0.602
winter 2015 @ 90 days $(Y)^{0.6}$	$F_{(1,8)} = 4.384$	0.070
spring 2015 @ 42 days $(Y)^{4.0}$	$F_{(1,8)} = 0.532$	0.487
spring 2015 @ 90 days	$F_{(1,8)} = 0.335$	0.579
summer 2016 @ 42 days $(Y + 0.1)^{0.6}$	$F_{(1,8)} = 0.415$	0.844
GROWTH OF TRANSPLANTED JUVENILE SPOROPHYTES		
autumn 2015 @ 42 days $(Y + 0.1)^{0.3}$	$F_{(1,58)} = 4.728$	**0.034***
autumn 2015 @ 90 days $(Y)^{0.15}$	$F_{(1,54)} = 1.826$	0.182
winter 2015 @ 42 days $(Y)^{0.05}$	$F_{(1,84)} = 1.504$	0.224
winter 2015 @ 90 days $(Y)^{0.1}$	$F_{(1,65)} = 0.007$	0.934
spring 2015 @ 42 days $(Y)^{0.25}$	$F_{(1,80)} = 7.235$	**0.009***
spring 2015 @ 90 days $(Y)^{0.4}$	$F_{(1,56)} = 1.070$	0.305
summer 2016 @ 42 days $(Y)^{0.15}$	$F_{(1,45)} = 0.017$	0.896

Adult sporophyte densities

The initial density of adults at the start of the experiment were mostly similar among patches, although somewhat elevated in the two smallest patches due to the calculation of density per metre-square (Fig. 3.3).

Density of adult sporophytes was relatively stable throughout the experiment, with the exception of the 0.1, 0.3 and 2.7 m^2 patches. These three patches typically had greater and more fluctuating densities of adult *E. radiata* (but again, we emphasise that fluctuations are accentuated dramatically by the need to scale to 1 m^2 area). Seasonal peaks in the density of adults were less clear than in juveniles. However, the maximum densities for the smallest patches tended to occur in summer and autumn 2015 (Fig. 3.3). Over the final 8 months of the study, the density of adult sporophytes in the three smallest patches slowly declined over time but were still equal to or higher than the other patches at the end of the study in summer 2016.

Transplanted macroscopic juveniles

There was no effect of patch size on the survivorship of the transplanted macroscopic *E. radiata* juveniles at either the 42 or 90-day period within seasons (Fig. 3.4) or when pooled annually (Table 3.3). Patch size did however affect the growth rates of the juvenile sporophytes transplanted during autumn 2015 and spring 2015, but only over the initial 42-day period (Fig. 3.5, Table 3.3), with no effect detected by the 90 day stage. No significant effects of patch size on growth rates were observed during winter 2015 or summer 2015.

Outplanted microscopic recruitment

Microscopic sporophytes were outplanted during spring in 2014 and 2015. During spring 2014, only 3 microscopic sporophyte recruits were observed on the control slides across all patches: two in the 0.3 m^2 patch, and one in the 73 m^2 patch. During this season, the number of surviving outplanted microscopic sporophytes decreased significantly with patch size (Fig. 3.6i, Table 3.4). During spring 2015, natural recruitment occurred across all but two patches with a total of 55 recruits, although this was not influenced by patch size (Table 3.4). Despite the non-significance, we still adjusted the counts of surviving outplanted microscopic sporophytes to account for background recruitment. During spring 2015, the adjusted number of sporophytes did not differ significantly across patch sizes (Fig. 3.6ii, Table 3.4), and the test result was the same if no adjustment was made. During spring 2015, approximately twice as many microscopic sporophytes survived across all patches compared to spring 2014 (930 vs 472), or 0.10 vs 0.05% survivorship respectively.

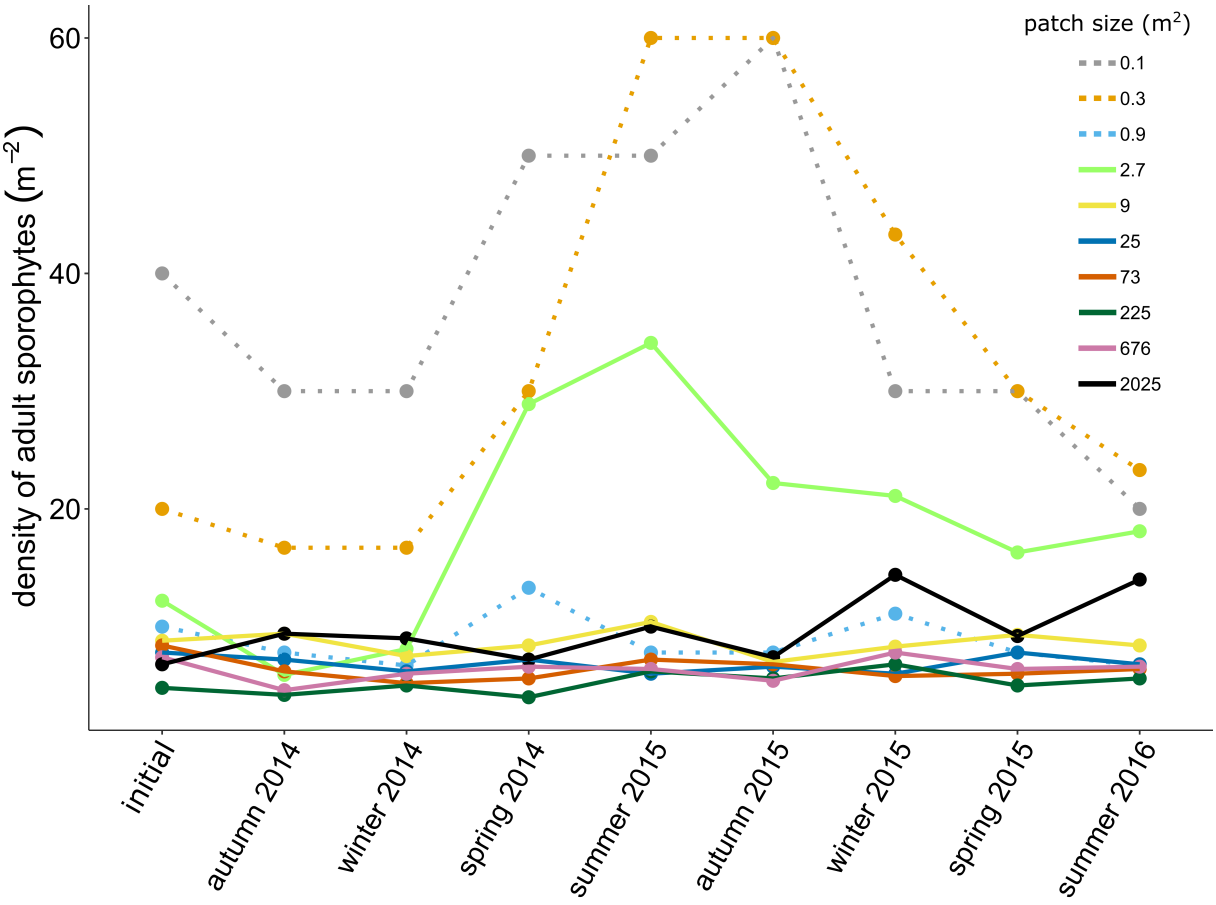


Figure 3.3 Time-series of adult *Ecklonia radiata* sporophyte density over 24 months for 10 different patch sizes. The three smallest patches that experienced an eventual collapse in recruitment (see Fig. 3.1) have dashed lines, and the remaining patches have solid lines

Table 3.4 Linear regression of recruitment and survival of microscopic *Ecklonia radiata* sporophytes against patch size, across 2 seasons. Response variable and associated transformation is noted in the first column. The factor, patch size, was $\log_3$-transformed to best meet test assumptions. Natural recruitment in spring 2014 could not be tested due to insufficient data. Significant relationships denoted in bold and with as asterisk.

data analysed	*F-value*	*P-value*
SPRING 2014		
natural recruitment	n/a	
survivorship $(Y+0.01)^{0.45}$	$F_{(1,8)} = 6.992$	**0.030***
SPRING 2015		
natural recruitment $(Y+0.01)^{0.25}$	$F_{(1,8)} = 0.046$	0.836
survivorship $(Y+0.01)^{0.25}$	$F_{(1,8)} = 0.555$	0.478

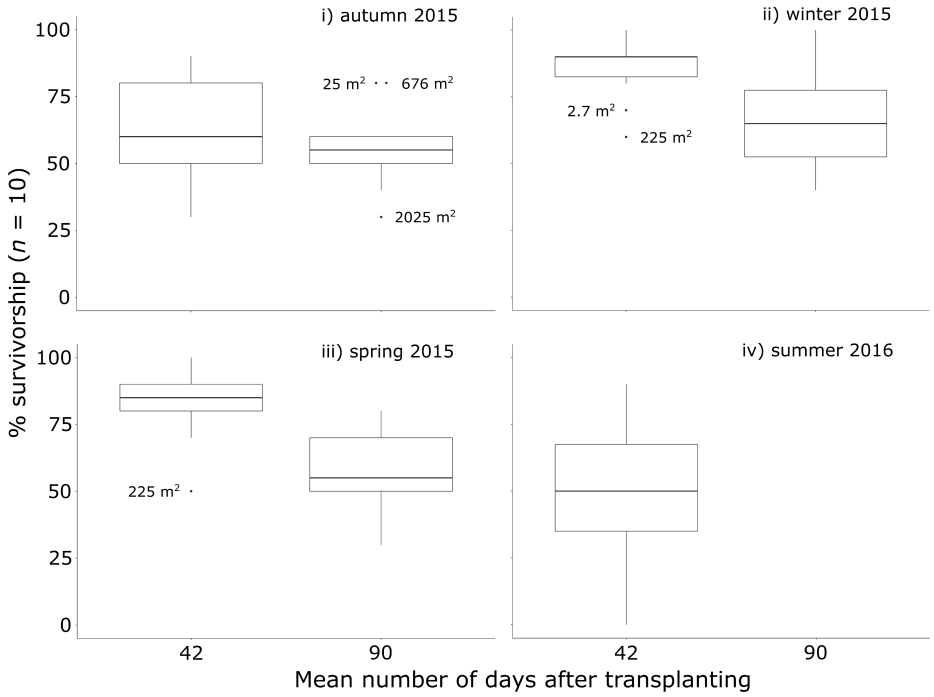


Figure 3.4 Survivorship of transplanted macroscopic juvenile *Ecklonia radiata* sporophytes across all 10 patches over four seasons (i–iv). Survivorship of juveniles was assessed ~42 and ~90 days after transplanting during each season, except for those transplanted in (iv) summer, which were only installed for the initial 42-day period. There were no significance differences in survivorship across patch size at either assessment within any season. The patch size of outliers is labelled.

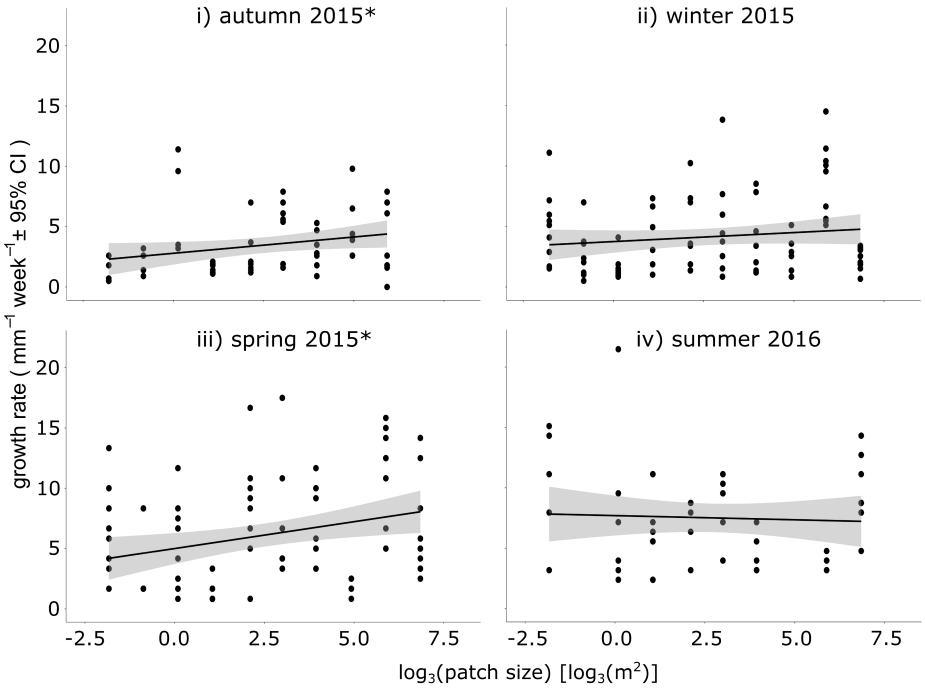


Figure 3.5 Linear regression of relationship between growth rates of transplanted macroscopic juvenile *Ecklonia radiata* sporophytes ~42 days after transplanting and patch size, across four seasons (i–iv). Seasons with significant relationships ($P < 0.05$) are denoted with as asterisk. Relationships between growth and patch size at ~90 days after transplanting were all non-significant (see Table 3.3).

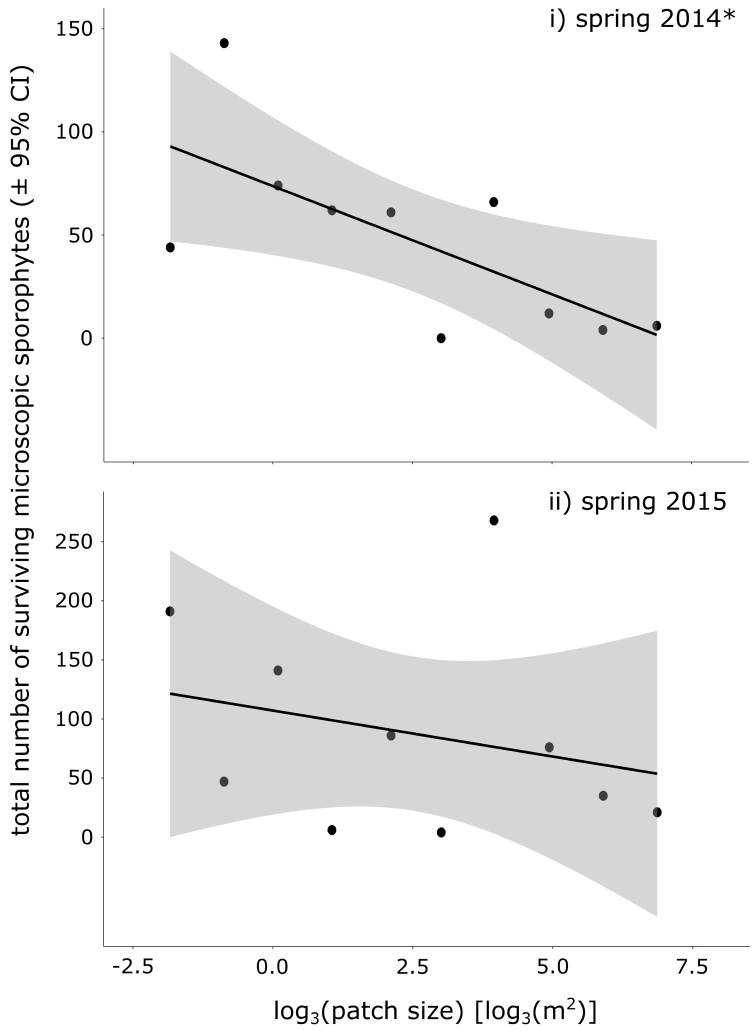


Figure 3.6 Linear regression of relationship between total number of surviving *Ecklonia radiata* microscopic sporophytes ~49 days after outplanting in (i) spring 2014 and (ii) spring 2015. Seasons with significant relationships ($P < 0.05$) are denoted with an asterisk.

Discussion

We observed that a persistent press disturbance – the reduction in the size of *Ecklonia radiata* patches – resulted in the eventual collapse of recruitment of juvenile kelp in patches smaller than 1 m^2. However, this disturbance initially resulted in a short-term increase in recruitment in those same patches. Experimental transplants of microscopic and macroscopic juvenile sporophytes did not identify the life stage impacted by the persistent reductions in patch size. This suggests the effects may be subtle and require longer periods to manifest, and/or that another life stage may be responsible. The results demonstrate the protracted effects of disturbance and the consequences of short and long-term degradation of *E. radiata* habitats.

Responses to disturbance

Following the initial disturbance of creating the patches, the four smallest patches (<3 m^2) experienced a rapid increase in the density of juvenile sporophytes. The swiftness of the response means these were unlikely to have originated from the settlement of novel kelp propagules. Instead, the pulse in recruitment most likely originated from the growth of pre-existing, but non-visible, sporophytes already within the sub-canopy (Kirkman 1981; Toohey & Kendrick 2007). Rapid growth/recruitment of pre-existing *E. radiata* sporophytes following disturbance (e.g. canopy-thinning or small-scale clearances) has been documented previously (see Kennelly 1987a; Flukes et al. 2014).

It is well recognised that juvenile *E. radiata* can arrest their development and persist within the sub-canopy environment until the onset of favourable conditions (Kirkman 1981; Toohey & Kendrick 2007). This phenomenon occurs in many large brown macroalgae, and the source of pre-existing individuals is often described as a 'seed bank' (Kinlan et al. 2003; Schiel & Foster 2006). Despite its ubiquity, there are few details known about the seed bank of most species of macroalgae (but see Edwards 2000; Kinlan et al. 2003), and it is unclear which life stage(s) of *E. radiata* can undergo arrested development and for how long. It is generally suggested however that the haploid gametophytes of most kelp cannot survive for extended periods in the field (Kinlan et al. 2003; Schiel & Foster 2006). This, coupled with our census of visible sporophytes (>5 mm) during patch creation, leads us to suspect that non-visible (i.e. <5 mm) or microscopic sporophytes populate the seed bank of *E. radiata*, and consequentially were responsible for the pulse in recruitment we observed. Kirkman (1981) observed that macroscopic juvenile *E. radiata* may also suspend their development within the sub-canopy, and so it is possible that multiple life stages contribute to the seed bank of this species. Investigation of this phenomenon in *E. radiata* and other kelp species represents a promising direction for future studies.

It is likely the seed bank represents a key life-history trait that aids rapid replenishment of the canopy following a pulse disturbance (Kirkman 1981; Kinlan et al. 2003), such as canopy removal due to storms (Toohey & Kendrick 2007; Flukes et al. 2014). This explains the rapid recruitment we observed following the removal of *E. radiata* canopy during the creation of the patches. The mechanism that drives the suspension and resumption of development is still unknown, but low and high light levels, respectively, are likely to be important drivers (Kirkman 1981; Johnson & Mann 1988; Kinlan et al. 2003). Indeed, within these same experimental patches we observed that sub-canopy irradiance significantly increased with reductions in patch size (Chapter 2). Moreover, the brighter sub-canopies of the smaller patches might explain why the recruitment pulse was only observed in the four smallest patches. Ultimately, this response led to the strong negative relationship between density of juvenile kelp and patch size at the first sampling period in autumn 2014.

After the initial pulse in response to patch creation, the density of juvenile sporophytes continued to rise for one more season across almost all patches, reaching peak density for many of the patches, including the four smallest. While these increases may have occurred due to delayed effects of the disturbance, it seems the continued increase more likely reflects juvenile kelp recruitment from the peak reproductive period from autumn (Mabin et al. 2013; Mohring et al. 2013). The lag between peak reproduction in autumn and the observed peak in recruitment was ~12.5 weeks, which provides an estimate of the time from sporulation to recruitment as a visible sporophyte. After this seasonal peak and onwards to spring 2014, the four smallest patches experienced dramatic declines in the density of juvenile *E. radiata.* This presumably indicated the exhaustion of the seed bank and the end of the seasonal peak in reproduction, but also, the loss of those previously recorded sporophytes from the juvenile cohort.

This decline in juvenile kelp density in the smallest patches continued and, 16 months after the creation of the patches, resulted in zero juvenile sporophytes in each of the three smallest patches. The strong negative relationship between juvenile kelp density and patch size that had been present since the start of the experiment changed abruptly to become significantly positive within the space of ~8 weeks. Moreover, this occurred just prior to the annual peak in recruitment that we had observed the previous year, indicating a collapse of this demographic process in patches below 1 m^2. For those patches that did not experience collapse, we observed the expected seasonal peak in recruitment throughout winter and spring 2015. During the final sampling period in summer 2016, the relationship between juvenile kelp density and patch size was non-significant, despite a positive trend. This non-significance was due to the influence of the fourth smallest patch on the analyses, which was a notable outlier (Table 3.2).

Examination of the different life-stages

The density of adult kelp (i.e. stages 2 & 3) changed throughout the experiment but was largely similar across patches and through time. The two smallest patches along with the 2.7 m^2 patch did vary more than the other experimental patches, but this was amplified by scaling of density to a standardised area (1 m^2) much larger than the patch size. Although typically not of equal magnitude, peaks in adult density lagged behind those of juvenile density by approximately two seasons or 25 weeks. This suggests a broad timeframe of development from stage 1 to stage 2 *E. radiata* at our site, which is longer than previous studies on *E. radiata* (e.g. Kirkman 1981). Although, slower rates of growth and maturation are not unexpected given that our sites are deeper and likely have less ambient irradiance (Novaczek 1984; Kirkman 1989).

The density of adult *E. radiata* is typically a strong predictor of the abundance of juvenile conspecifics, with denser canopies typically associated with fewer juvenile sporophytes (Kirkman 1981; Kennelly 1987a). This clearly does not apply in our small patches, which had high densities of

both adult and juvenile *E. radiata* (Figs. 3.1, 3.3). Whilst partially influenced by the artefact of standardisation, this likely occurred because adult kelp density becomes less relevant in small patches where edge effects are more pronounced (Dayton et al. 1984; Angelini & Silliman 2012). The combined effects of density and patch size on the demography of *E. radiata* remain to be tested but are of importance considering kelp habitat degradation often manifests as reductions in both these key habitat characteristics.

The higher densities of juvenile kelp in the smaller patches did partly translate to increased adult kelp density, although clearly not every juvenile sporophyte survived to enter the adult cohort (c.f Figs. 3.1, 3.3). One anomaly was the fourth smallest patch (2.7 m^2) however, which had a maximum adult kelp density higher than its maximum juvenile kelp density. Kelp density in this patch was censused, so this could have only occurred by juveniles developing from non-visible to stage 2 sporophytes over the ~12.5-week period between samples, which is possibly (see Kirkman 1981). This patch did indeed have a greater proportion of stage 2 sporophytes in the adult cohort than other patches (pers. obs.). Nevertheless, the overall lack of a pattern between peak density of juveniles and adults in each patch indicates there must be high mortality of stage 1 sporophytes.

While we did observe mortality in our transplanted macroscopic juveniles (Fig. 3.4), there were no differences in survivorship related to patch size. The sporophytes were installed for a total of ~90 days, which is approximately half of the 25 weeks we estimated that it typically takes stage 1 sporophytes to develop to stage 2. Therefore, it is possible that a longer installation period was required to detect differences across treatments. Parallel observations in these experimental patches detected that smaller patches had significantly higher levels of sub-canopy irradiance and water flow (Chapter 2), both of which are potential stressors of juvenile *E. radiata* (Wood 1987; Eckman et al. 1989; Toohey & Kendrick 2007). Importantly, the negative impacts from abiotic stressors may be subtler on deeper reefs such as those studied here and require longer timeframes to induce responses (Novaczek 1984; Dayton et al. 1992). It would therefore be valuable to repeat this experiment in a shallower environment. We did detect that growth rates of the transplanted macroscopic juvenile sporophytes increased significantly with patch size on some occasions when measured over a 6-week period (Table 3.3). Whilst this effect was not seasonally consistent nor persistent, it may indicate that stage 1 sporophytes in smaller patches require longer to develop and become reproductively viable (Novaczek 1984). It also suggests that the observed decline in juvenile kelp density in the small patches was not due to their accelerated development into the adult cohort.

In summary, while macroscopic juvenile *E. radiata* may experience delayed growth and maturation in small patches, we detected no effect of patch size on their survivorship. Thus, the long-term decline and abrupt absence of juvenile kelp we observed is more likely due to a decline in

ongoing recruitment, i.e. where the removal of kelp from the juvenile cohort (due to growth and mortality) is not replenished by the recruitment of new sporophytes.

However, survivorship of the outplanted microscopic sporophytes was significantly higher in the smaller patch sizes during spring 2014 (Table 3.4). The lower amounts of kelp scour or higher sub-canopy irradiance in these patches may have benefitted the developing microscopic sporophytes (Dayton et al. 1984; Chapter 2). In contrast, patch size had no influence on survivorship of the microscopic sporophytes during the second outplanting trial in spring 2015, and similarly, in the one season we observed substantial natural recruitment onto the blank microscope slides (spring 2015) we detected no effect of patch size. Ultimately, patch size had inconsistent effects on microscopic sporophytes and, whilst there was an indication small patches became less suitable for microscopic sporophytes over time, outplanting over only two periods was not adequate to explore this fully.

Spore supply, the sub-canopy environment, and habitat resilience

Irrespective of the life stage involved, the smallest patches eventually experienced a collapse in the recruitment of juvenile *E. radiata*. This is especially striking considering that the experimental patches were embedded within a large stand of *E. radiata*. As such, the smallest patches would not have suffered the reduced supply of propagules that would be expected had they been isolated by distance from other kelp (Reed 1990; Santelices 1990). Indeed, diminished propagule supply and poor patch connectivity are expected to be challenges in fragmented kelp habitats (Dayton et al. 1984; Reed 1990; Coleman et al. 2009). This may especially be the case for species with short dispersal distances, where reproductive isolation can occur with even minor levels of habitat degradation (Dayton et al. 1984; Coleman et al. 2009; Bennett & Wernberg 2014).

Nonetheless, each experimental patch likely had a similar level of propagule supply (given the proximity of the surrounding stand of *E. radiata*), so we conclude that supply-side dynamics were not responsible for the collapse in recruitment we observed in the smallest patches. Overall, it seems that the only difference between patches where recruitment collapsed, and those where it did not, was the physical environment in which the propagules settled.

This occurred because the capacity of *E. radiata* to act as an ecosystem engineer and modify the abiotic environment is reduced in smaller patches (Chapter 2). Parallel study of these patches highlighted that small patches had significantly altered abiotic conditions, with increased levels of sub-canopy sedimentation, irradiance and water flow, and decreased kelp scour (Chapter 2). This follows Bender et al. (1984), who suggests the overall impacts from press perturbations involve the combination of direct effects with indirect effects that are mediated through other species and processes. To this end, increased sub-canopy flow may negatively influence settlement dynamics (Eckman et al. 1989), but can also exacerbate the negative effects of other stressors such as irradiance

(Toohey & Kendrick 2007) and sedimentation (Devinny & Volse 1978). Similarly, increased irradiance can be a direct stressor on microscopic and macroscopic juvenile kelps (Wood 1987; Altamirano et al. 2004), but also promotes the establishment of the turf algae that trap deleterious sediments (Kennelly 1989; Irving & Connell 2006). Indeed, increased accumulation of sediments in the smaller patches – typically trapped within the filamentous turf algae – may be of particularly importance.

It is well recognised that sediments inhibit the recruitment of *E. radiata* and other kelp, possibly through smothering, abrasion, and substratum instability (Devinny & Volse 1978; Kennelly 1987b; Watanabe et al. 2016). The trend of increased sediment accumulation in the smaller patches first became significant during spring 2015 (Chapter 2), which was the period immediately following the crash in recruitment. Moreover, the depth of the sediments within the patches increased over time throughout 2015 (Chapter 2). This seems to illustrate that the sub-canopy environment was slowly changing over time and suggests that perhaps a threshold in the cover and/or depth of the developing matrix of turf algae and trapped sediments was reached, leading to persistent deterioration in recruitment of new kelp. The increased sub-canopy irradiance and decreased kelp scour that we observed in smaller patches (Chapter 2), is the likely mechanism that led to increased cover of the filamentous turf algae, which are fundamental to the entrainment and consolidation of sediment particles on the benthos (Kennelly 1989; Irving & Connell 2006). Notably, turf algae tend to be less productive and prevalent on deeper reefs (Copertino et al. 2005), likely due to decreased irradiance, which may explain why turf algae were slow to establish in our patches. This may also explain why we detected no effects of patch size on natural recruitment, because the blank microscope slides were not immersed for sufficient time to develop a representative cover of turf algae. If this hypothesis is correct, we would expect to see a faster response within shallower environments.

What is apparent from our results are the nonlinear responses to patch size, further suggesting the existence of potential thresholds. The nonlinear relationship between patch size and the density of newly recruited kelp was very strong immediately following patch creation and became weaker and more linear as time progressed. Of particular interest is that the fourth smallest patch (2.7 m^2) responded to the initial disturbance following patch creation but did not experience the same breakdown in recruitment. This may represent a critical threshold patch size where ecosystem engineering by *E. radiata* was just sufficient to maintain the sub-canopy environment and ensure patch resilience. The eventual failure in kelp recruitment in the smaller patches seems to represent another critical threshold. This appears to be linked to increasing sediment accumulation within the smallest kelp patches, which is consistent with dramatic phase shifts of structurally complex, productive and biodiverse kelp ecosystems to less complex, less biodiverse and less productive turf-dominated ecosystems (Strain et al. 2014; Wernberg et al. 2016).

Our results suggest that habitat fragmentation has the potential to influence the long-term resilience and stability of *E. radiata* habitats by disrupting recruitment. While reductions in patch size did initially cause an increase in recruitment, this response was likely from the existing seed bank. It seems unlikely that the 'seed bank effect' could facilitate longer-term resilience to a press perturbation, given impaired settlement and recruitment as the turf-sediment matrix develops and thus poor/no replenishment of the seed bank (Kirkman 1981; Kinlan et al. 2003; Strain et al. 2014). Smaller kelp patches may also be less likely to recover even after the perturbation has ceased (Angelini & Silliman 2012). In this instance, reductions to kelp patch size disrupt the juvenile cohort, leaving the adult cohort unable to sufficiently and promptly replenish the population (Wernberg et al. 2010). This may lead to post-disturbance kelp populations that consist only of adult kelp that will perish after one generation. Such demographic disruptions may be difficult to detect (Caley et al. 1996) but could represent appropriate situations for human intervention and ecological restoration (Johnson et al. 2017).

Conclusion

We demonstrate that persistent reductions in patch size, like those resulting from many anthropogenic stressors, can lead to the collapse of recruitment in patches of *E. radiata* smaller than 1 m^2. Importantly, we observed that collapse can occur even without the compromised propagule supply that is expected in small patches of kelp that are reproductively isolated from conspecifics. The impaired ability of *E. radiata* to engineer abiotic change within small patches seemingly leads to the degradation of the sub-canopy environment over time. This resulted in proliferation of turf algae and entrained sediments in small patches, which we suspect ultimately disrupted the settlement and recruitment of juvenile kelp. Notably, the initial response to the disturbance of patch creation was a pulse increase in recruitment in patches smaller than 3 m^2. This interesting dual-response – a potential short-term resilience mechanism to pulse disturbances, but also an eventual cessation of recruitment – highlights the importance of long-term observations in the field. We suspect that the depth of the experimental patches may have contributed to the protracted response we observed, chiefly because of the lower amount of irradiance and the slower formation of the turf algae necessary to capture sediments. We conclude that habitat fragmentation can cause severe disruptions to the demography of *E. radiata* in smaller kelp patches. This has clear consequences for habitat resilience and recovery of kelp habitats in the face of increasing anthropogenic threats.

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Chapter 4. Resilience and stability of kelp forests: the importance of patch dynamics and environment-engineer feedbacks

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Abstract

Habitat-forming 'ecosystem engineers' such as kelp are of disproportionate importance to ecosystem health and functioning because they create physically complex habitats and a range of microenvironments that support biodiverse and productive communities. Studies of the resilience and stability of ecosystem engineers have typically focussed on the role of external factors such as disturbance. However, their population dynamics are also likely to be influenced by endogenous processes, such that the environmental modifications caused by engineer species feedback to affect its own demography (e.g. recruitment, growth).

Kelp forests around the world sustain hugely productive ecosystems with high levels of biodiversity and economic value. However, in numerous regions globally kelp forests are in decline and experiencing reductions in patch size and kelp density. To explore how the resilience and stability of the kelp *Ecklonia radiata* is influenced by this habitat degradation, we created an array of artificial patch reefs of various sizes spread over 1.5 ha and supporting adult *E. radiata* transplanted at different densities. This unique environment enabled testing of how sub-canopy abiotic conditions change with reductions in patch size and adult kelp density, and how these changes influenced fundamental demographic processes of both the microscopic and macroscopic juvenile *E. radiata* (including recruitment, survivorship, growth).

We found that ecosystem engineering by *E. radiata* modified the local environment to reduce water flow, sedimentation and irradiance within the sub-canopy. However, the capacity of the kelp to engineer abiotic change was largely dependent on patch size, and to a lesser extent, kelp density. The recruitment, growth and survivorship of microscopic and macroscopic juvenile *E. radiata* were also all impaired by reductions in patch size and kelp density, and even after the provisioning of

established propagules and juveniles, many of these demographic processes collapsed in the absence of sufficient adult kelp.

Our results are consistent with the hypothesis that ecosystem engineering by adult *E. radiata* facilitates the development of juvenile conspecifics. However, habitat degradation can impair the ability of *E. radiata* to engineer change, causing a breakdown in the positive feedback and collapse of demographic functions, which overall, lead to reduced ecosystem stability and resilience.

Introduction

Coastal marine ecosystems are under threat from a variety of anthropogenic stressors including urbanisation, pollution and climate change (Airoldi 2003; Hughes et al. 2003; Krumhansl et al. 2016). One of the critical effects of these stressors is to reduce the extent and abundance of habitat-forming species, or 'ecosystem engineers' (e.g. coral, kelp, seagrass; Pandolfi et al. 2003; Wernberg et al. 2016). These species are of disproportionate importance to the health and function of ecosystems because they create physically complex habitats that support biodiverse and productive communities (Jones et al. 1994; van der Zee et al. 2016). In some cases, anthropogenic and environmental stressors can trigger declines in the abundance of ecosystem engineering species to a point where complex and diverse ecosystems 'phase shift' to become structurally simple, less diverse and less productive environments (Connell et al. 2008; Ling et al. 2009; Mumby 2009; Fung et al. 2011). It follows that informed management and conservation of coastal marine environments requires thorough understanding of the stability and resilience of marine ecosystem engineers.

Ecosystem engineers modify the properties of the local environment in three main ways: structural engineering (changes in habitat structure, e.g. provision of physical complexity); abiotic engineering (changes to the abiotic environment, e.g. light, water flow, nutrients); and biotic engineering (changes in biota as a response to structural or abiotic engineering) (Jones et al. 2010). These environmental modifications have major consequences for the ecological community and can alter resource flows (Jones et al. 1997), ameliorate physical stressors (Crain & Bertness 2006), and promote biodiversity (Romero et al. 2015). Far less attention however has been given to how engineering of the environment feeds back to influence the engineer itself, i.e. the so-called 'environment-engineer feedback' (Jones et al. 2010). These feedbacks occur when the demography of the engineer is itself affected by the environment it engineers, and intraspecific facilitation arising from environment-engineer feedbacks is likely to apply to many habitat-forming species that reproduce, recruit, and grow in the engineered habitat (Bulleri 2009; Cuddington et al. 2009; Jones et al. 2010).

However, environment-engineer feedbacks are likely to be complex, and this arises from several sources. Firstly, because of the multiple mechanisms by which environment-engineer

feedbacks can occur (i.e. structural, abiotic, biotic) there is potential for additive, synergistic or interactive effects among the separate mechanisms (Jones et al. 2010). Secondly, considering the importance of patch size in influencing fundamental community properties (Sousa 1984; Wright et al. 2004; Dunstan & Johnson 2006) and that ecosystem engineering is often density-dependent (Wernberg et al. 2005), it follows that environment-engineer feedbacks are also likely to be patch size and density-dependent. Lastly, ecosystem engineering is likely to be context-dependent, varying with the environmental conditions (Jones et al. 2010). This will arise if gradients in abiotic factors influence engineer density or patch size, and/or if engineering of abiotic factors become more important in more extreme environments (Crain & Bertness 2006; Bennett et al. 2015). While this complexity is recognised at a theoretical level, the net consequences of these feedbacks for species have not yet been explored empirically.

Kelp (Order Laminariales) are ecosystem engineers that provide habitat through their own physical presence and modify abiotic conditions such as light, sedimentation and water flow (e.g. Kitching 1941; Eckman et al. 1989; Wernberg et al. 2005). Kelp forests around the world sustain highly productive ecosystems that provide a range of physical habitats and support high levels of biodiversity and economic value (Steneck & Johnson 2014; Schiel & Foster 2015; Teagle et al. 2017). However, in numerous regions globally kelp forests are in decline, with habitats experiencing reductions in patch size and kelp density (Johnson et al. 2011; Steneck & Johnson 2014; Krumhansl et al. 2016). It is therefore imperative to develop understanding of how the resilience and stability of kelp as marine ecosystem engineers is influenced by habitat degradation and anthropogenic stressors.

The kelp *Ecklonia radiata* is the most widespread habitat-forming macroalga in Australasia. This species dominates the Great Southern Reef – Australia's continental wide temperate reef system – and supports high levels of biodiversity, endemism and productivity (Bennett et al. 2016). This stipitate kelp (*sensu* Dayton et al. 1984) rarely grows taller than 1.5 m, but creates dense and spatially complex habitats with levels of productivity that equal or exceed many other kelp species (Larkum 1986: Hatcher et al. 1987). Like many kelp globally, this species too is under threat from rising ocean temperatures, overgrazing from invasive and range-expanding species, and urbanisation and pollution (Connell et al. 2008; Ling et al. 2009; Vergés et al. 2016; Wernberg et al. 2016). As a result, *E. radiata* is becoming increasingly sparse and patchy in many locations across its range. A major impediment to managing, conserving and restoring these ecologically, socially and economically valuable ecosystems is poor knowledge of the mechanisms underpinning their stability and resilience (Evans et al. 2017).

Existing research into the resilience of *E. radiata*, and most other marine ecosystem engineers, has focussed primarily on their response to external processes such as disturbance or interspecific interactions (e.g. Kennelly 1987a; Steneck et al. 2002; Toohey & Kendrick 2007).

Despite this, it seems that internal drivers influencing *E. radiata* demography, and particularly positive environment-engineer feedbacks, are equally important. Indeed, breakdown of positive environment-engineer feedbacks due to a reduction in patch size or adult density may explain the slow recovery of *E. radiata* often observed after large-scale losses (e.g. Kirkman 1981; Toohey et al. 2007; Connell et al. 2008). Further, there are a number of important gaps in the current understanding of *E. radiata* demography and there have been few demographic studies of the species' microscopic life stages, particularly involving the recruitment and survival of microscopic sporophytes *in situ* (but see Tatsumi & Wright 2016).

This study determined how ecosystem engineering by *E. radiata* is affected by reductions in patch size and kelp density, and whether this feeds back to influence the species' demographic rates. We created an array of artificial reefs of different sizes onto which adult kelp were transplanted at a range of densities. Specifically, we examined (i) how the physical environment beneath *E. radiata* canopies changes with reductions in patch size and adult kelp density and, (ii) how these changes affect fundamental demographic processes of microscopic and macroscopic juvenile *E. radiata* including recruitment, survivorship and growth. In the face of increasing anthropogenic pressure on *E. radiata* and other kelp, our aim to address whether habitat degradation reduces kelp forest resilience and stability due to a breakdown in intraspecific facilitation and environment-engineer feedbacks.

Methods

Site and artificial reefs

The experimental site (-42.64693, 148.01481) was a flat, sandy embayment off the coast of Maria Island on the east coast of Tasmania, Australia. This area was selected for its uniform depth (6.5 m) and isolation from any natural rocky reefs (>1.5 km). Divers using SCUBA installed artificial reefs at the site that provided structure and substrata for transplanting kelp. The reefs were constructed in seven patch sizes, 0.12, 0.24, 0.48, 1.08, 1.92, 4.32 and 7.68 m^2, which were crossed with four kelp density treatments to produce 28 experimental patch reefs with a total combined area of ~63 m^2. Each patch had a length-width ratio of approximately 4:3.

The reefs were installed in December 2014 in a grid formation consisting of 5 columns and 6 rows and spanning more than 12,500 m^2 (Fig. 4.1). Each reef was randomly allocated a position within this grid and separated from neighbouring reefs by 25 m. Dispersal distances in kelp are typically proposed to be short and occur over metres (Dayton et al. 1984; Reed et al. 1988; Schiel & Foster 2006), and although longer distance dispersal can occur under certain conditions, molecular data suggests low dispersal in *Ecklonia radiata* (Coleman et al. 2009). As such, each reef was considered isolated from receiving meaningful amounts of spores from neighbouring reefs (see 'Results' for confirmation of this assumption).

Reefs consisted of a steel frame and concrete pavers. The frame was elevated on legs 30 cm above the substratum to eliminate sand inundation and allow drift algae to pass underneath. Turfstone pavers (400 x 300 x 100 mm, L x W x H) with a topside surface area of 0.12 m^2 were secured to the steel frame and were chosen due to their shape, which provided physical complexity and interstitial crevices (Fig. 4.2).

Kelp transplanting

Adult *E. radiata* were transplanted onto the experimental patches at four different densities, which were based on a mean density of adult kelp on nearby natural reefs of ~8/m^2 (Johnson & Layton unpubl. data). The treatment levels were no kelp, half-natural, natural, and double-natural kelp density. Due to the constrained dimensions of the pavers, the specific kelp densities were 0, 4.1, 8.3 and 16.6 kelp/m^2 (hereafter called zero, half, natural and double density respectively). Stands of *E. radiata* across Australia naturally contain areas with this range of adult kelp densities (Kirkman 1981; Wernberg et al. 2005; Flukes et al. 2014).

Adult sporophytes were collected at depths 4–8 m from the closest extensive stand of *E. radiata* (-42.73138, 148.01045), which was ~9 km from the experimental site, and transplanted onto the reefs during January and February 2015. All transplanted *E. radiata* were stage 3 adult sporophytes (*sensu* Kirkman 1981) and were selected based on two requirements; (1) stipe length between 150–300 mm, and (2) lamina and stipe free of substantial epibiotic growth or degraded tissue. Suitable sporophytes were collected by removing their holdfast from the rock substratum using a blunt-tip knife, and any additional macroalgae attached to the holdfast, including other *E. radiata*, were discarded. Collected kelp were placed in large opaque bags, transported to the experimental site and transplanted generally within 6 hours (always <18 hrs) of collection.

Holdfasts of transplanted kelp were secured to the reefs using large rubber bands and Z-SPAR Splash Zone epoxy. After 4–6 weeks, newly developed haptera had reattached the transplanted sporophytes to the concrete pavers. In total, 462 adult sporophytes were initially transplanted to the experimental site. Kelp density treatments were reassessed every 6 weeks and any adult sporophytes that had been lost were replaced. Replacement kelp were collected using the same methodology as outlined above but were secured to the reefs using the rubber bands only, as the epoxy was found to be unnecessary.

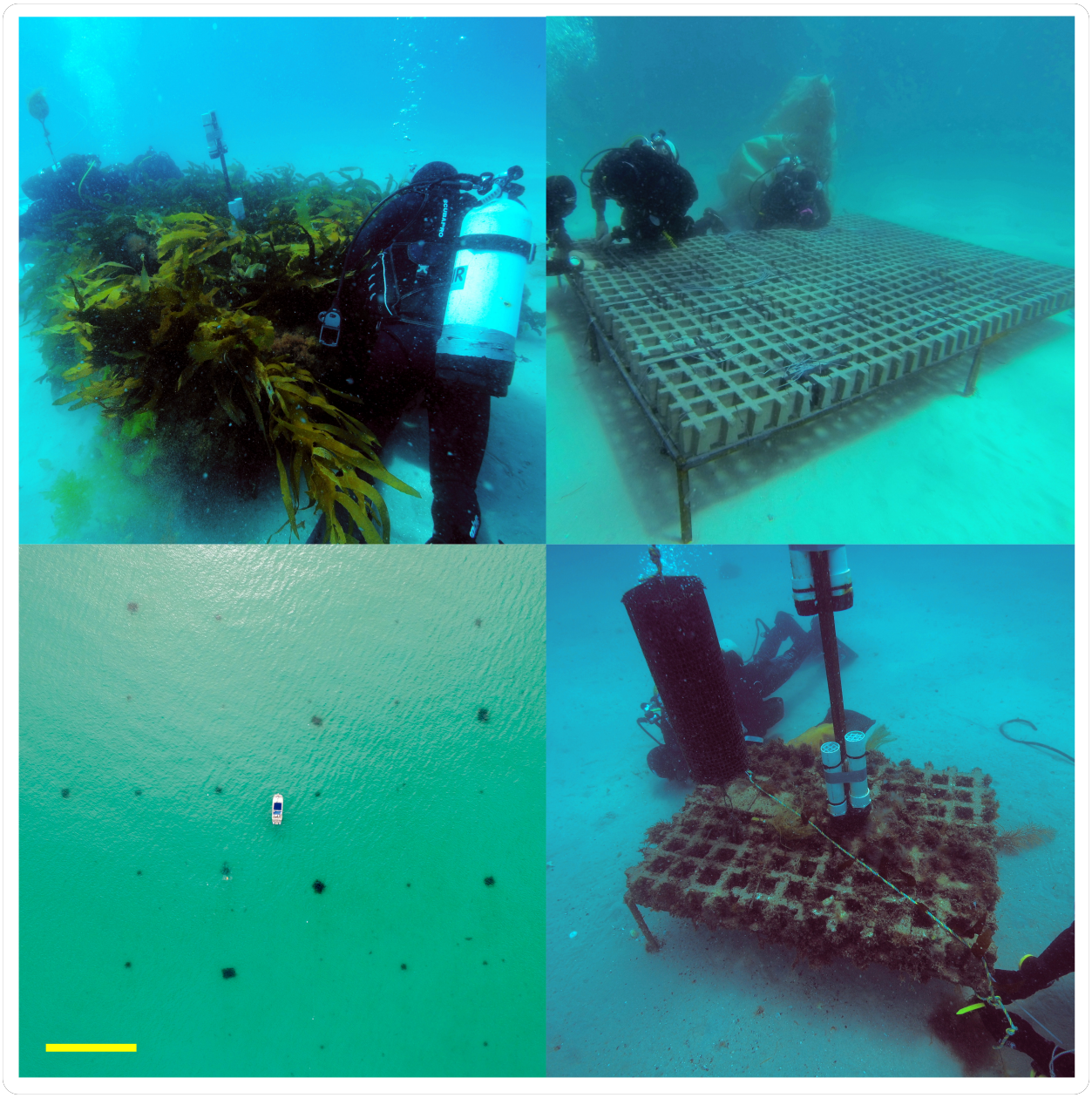

Figure 4.1 Experimental patch reef array. Clockwise from top left: a 7.68 m^2 patch reef with transplanted kelp; a 7.68 m^2 patch reef during construction; a 1.08 m^2 patch reef with no transplanted kelp, and; an aerial photo of the grid formation of experimental patch reefs (yellow scale bar represents 25 m).

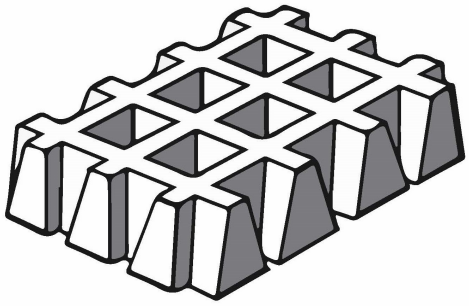

Figure 4.2 Concrete Turfstone® paver of dimensions 400 x 300 x 100 mm (L x W x H) used in construction of the experimental patch reefs. Image modified from Adbri Masonry.

Abiotic measurements

Sediment deposition

Sediment deposition was measured using sediment traps constructed from PVC piping. See Chapter 2 for trap details. Sediment traps were installed in autumn (April), winter (July), spring (September) and summer (December) for a period of 41 days (± 2, SE). Four traps were positioned in the approximate centre of each patch, with two traps above the kelp canopy and two below. Above-canopy traps acted as controls to measure background rates of sediment deposition, while sub-canopy traps measured any treatment effects.

For collection, sediment traps were sealed underwater before being retrieved to the surface and transported to the lab. Trap contents were flushed into pre-weighed foil trays and dried at 70ºC until a constant mass (~48 hours). The dried sediments were weighed on a laboratory balance to 0.01 grams and a rate of deposition above and below the kelp canopy in each patch was calculated based on the mean dry mass of the sediment from the two traps in each position (g day^{-1} m^{-2}). When a trap was lost or unsuitable for analysis (e.g. due to octopus habitation), the sediment mass was calculated from a single trap. Dried sediments were sieved through 250 and 62 μm mesh to examine their composition.

Sediment accumulation

The depth of accumulated sediments covering the substratum was measured to the nearest 1 mm using a small ruler at five locations in each patch – one in the approximate centre of the patch and four more at randomly selected compass marks approximately halfway to the patch edge. Sampling occurred in spring (September) and summer (January).

Water flow

The dissolution of clod cards (plaster blocks) was used to determine relative differences in sub-canopy mass transfer. For the sake of communication, mass transfer is hereafter referred to as water flow, but we acknowledge the difference of these processes (see Thompsen & Glenn 1994; Porter et al. 2000). See Chapter 2 for clod card details.

Each clod card was mounted to a thin plastic base and installed in the centre of each patch, attached either to the substratum or to a bracket atop the sediment trap array. These positions represented sub-canopy and above-canopy environments respectively. The clod cards positioned above the canopy acted as controls that measured ambient water flow, while those below the canopy measured any treatment effects. All clod cards were fitted with a coarse mesh guard to protect them from the confounding effects of erosion due to kelp scour. After ~72 hours *in situ,* the clod cards were collected and dried at 50° C for 24 hours and re-weighed. Due to inconsistencies in the plaster, the

initial masses of clod cards varied by ~15% and so mass loss was standardised as a percentage of mass lost. Preliminary testing revealed no relationship between initial mass and magnitude of mass lost.

Clod cards were installed during winter (June) and spring (September). These are the seasons of maximum water motion in Tasmania due to seasonal storms and winds, and the peak period for *E. radiata* spore release and recruitment of juvenile sporophytes (Kennelly 1987a; Mabin et al. 2013; Mohring et al. 2013).

Irradiance

Photosynthetically Active Radiation (hereafter, irradiance) was measured as Photosynthetic Photon Flux Density using a LI-COR LI-1500 Light Sensor Logger and LI-193 Spherical Underwater Sensor. This 330º sensor allowed measurements of the incidental irradiance that entered through the sides of the kelp patches. The sensor was secured to a 1.8 m pole to minimise diver interference, and the irradiance in the centre of each patch was recorded for 60 seconds above and below the kelp canopy. Irradiance was automatically logged every 15 seconds as mean μmol photon m^{-2} s^{-1}, providing four mean measures per position over the 60-second sample. Above-canopy measurements provided ambient irradiance and acted as controls, while sub-canopy readings measured any treatment effects. The measurements were taken on a sunny day in spring (November) between 1030–1430 hours. Preliminary analyses confirmed no significant effect of time of day on the measurements.

Kelp demographics

Macroscopic juvenile sporophytes

Macroscopic juvenile *E. radiata* sporophytes were transplanted onto a subset of patches and their survivorship and growth determined for a 3-month period. We used a subset of patches (Table 4.1) due to limitations in the number of juveniles that could be collected. In autumn (April) we focussed on all patch sizes from the natural density treatment. In an effort to determine kelp density effects, the subset of patches for the following seasons (winter, spring and summer) included all kelp density treatments but fewer patch sizes (Table 4.1). Storms prevented the collection of sufficient data during winter, so no data were analysed from that season.

For transplanting, stage 1 juvenile sporophytes (50–150 mm in length) were collected from the same site as the adult kelp. Each juvenile was measured to the nearest 2 mm and hole-punched at the base (i.e. proximal end) of the lamina above the meristem to determine growth. Ten juvenile sporophytes were then threaded at 100 mm intervals into the twine of nylon rope, and one rope secured in the centre of each experimental patch. After 40 ± 3 days (SE), the growth – measured from the top of the holdfast to the base of the punched-hole – of each transplanted juvenile was measured to the nearest 2 mm *in situ*, and the sporophyte hole-punched again in the original proximal position. If a

sporophyte was missing, the position was noted, and the individual recorded as not surviving. After 90 ± 9 days (SE), the ropes were collected, and growth and survivorship determined again. Pilot studies confirmed that growth measurements were identical regardless of whether they were made *in situ* or *ex situ*. Only the growth rates and survivorship after 90 days were used for analyses, with the growth rates calculated by summing the ~40-day and ~90-day growth measurements and expressed as mm/week. Preliminary analyses revealed growth rates of sporophytes were linear and independent of initial sporophyte length.

Table 4.1 The experimental subsets into which macroscopic juvenile sporophytes were transplanted each season (*N* = total number of reefs). Winter sampling was attempted, but storms prevented the collection of sufficient data.

season	*kelp density (kelp/m^2)*	*patch size (m^2)*	*N*
autumn	natural (8.3)	all patch sizes	7
spring	zero (0)	0.48, 1.08, 4.32	3
	half (4.1)	0.48, 1.08, 4.32	3
	natural (8.3)	0.12, 0.48, 1.08, 4.32, 7.68	5
	double (16.6)	0.48, 1.08, 4.32	3
summer	zero (0)	0.48, 1.08, 4.32	3
	half (4.1)	0.48, 1.08, 4.32	3
	natural (8.3)	0.12, 0.48, 1.08, 4.32, 7.68	5
	double (16.6)	0.48, 1.08, 4.32	3

Microscopic sporophyte recruitment and survivorship

Like all kelp, mature *E. radiata* sporophytes release motile zoospores that settle and germinate into male or female gametophytes (Reed 1990; Schiel & Foster 2006). Once fertilised the female gametophyte provides the base from which the microscopic sporophyte develops. Lab-cultured microscopic sporophytes were outplanted during annual peak recruitment in winter (June) to determine their survivorship across patch size and adult density. Blank microscope slides were deployed at the same time to measure the natural background recruitment of microscopic *E. radiata* sporophytes.

Reproductive tissue for culturing was collected from stage 3 *E. radiata* at the collection site, and culturing followed the methods of Mabin et al. (2013) and Tatsumi & Wright (2016). Briefly, zoospores at a density of ~7000/mL were settled onto fully-frosted microscope slides submerged in UV-sterilized and filtered (0.2 μm pore-size) seawater, and the culture maintained for 43 days. Following this incubation period, 10 randomly selected slides were assessed under a microscope to determine mean sporophyte abundance prior to outplanting, which was ~7700 (± 550, SE) sporophytes per slide. Six randomly selected slides with cultured sporophytes, and two blank fully-frosted microscope slides (which had been curing in filtered seawater during the culturing process) were then attached in random order to a plastic rack. The racks were transported to the experimental

site submerged in seawater in an insulated container. At the site, divers attached two racks (i.e. 12 slides supporting sporophytes and 4 control slides) in the approximate centre of each patch. After 42 days, the racks were collected and transported to the lab where all surviving sporophytes on the slides were counted. Efforts were made to also record any naturally recruited gametophytes, but due to their very small size (typically <200 μm) it was not possible to accurately and reliably count them on the fouled microscope slides. The duration of the outplanting was sufficient for naturally settled zoospores to have developed into microscopic sporophytes (Schiel & Foster 2006; Mabin et al. 2013).

Recruitment of macroscopic sporophytes

The natural recruitment of macroscopic juvenile sporophytes onto each patch was determined via visual census. During a timed search (5 seconds per paver) all visible (approximately >5 mm) stage 1 *E. radiata* sporophytes were counted cross the entire patch. These censuses were conducted by the same individual (CL) and occurred during peak recruitment in spring (November) and the following winter (June). Census of stage 1 juveniles on all patches also occurred when patches were destructively sampled at the end of the study in spring (November) 2016. Recruit density (sporophytes/m^2) was used as the response variable for testing; however, we also present the absolute number of recruits for completeness

Data analysis and statistics

Because our first aim was to test the ecosystem engineering capacity of *E. radiata*, we tested measures of sub-canopy light, sediment deposition and water flow relative to the above-canopy environment. Preliminary tests indicated there were no effects of patch size or kelp density on any above-canopy abiotic conditions (Appendix 4.1). We still present absolute values of abiotic conditions where applicable in order to describe the sub-canopy environment.

Because macroscopic juvenile *E. radiata* were not transplanted into all patches each season (see Table 4.1), and poor survivorship in some treatments (see Results), it was not possible to analyse all planned treatment combinations. Consequently, we analysed: (i) whether survivorship differed among all seven patch sizes when adult kelp was at natural density; (ii) whether survivorship differed among the four kelp density treatments using the subset of patch sizes from spring and summer (Table 4.1), and; (iii) whether survivorship differed across all 3 seasons using the subset of patches when kelp was at natural density. Analysis of growth rates of these transplanted macroscopic juveniles necessitated a similar approach, and we tested: (i) whether growth rates differed across all seasons using the subset of patches when kelp was at natural density; (ii) whether growth rates differed among the four kelp density treatments using the subset of patch sizes from spring only, and; (iii) whether growth rates differed among juveniles transplanted onto to reefs with transplanted kelp (i.e. zero density was omitted) during spring and summer.

Data were primarily analysed using Analysis of Covariance (ANCOVA) with patch size as a Model I (i.e. fixed) covariate. Model factors were all fixed and are described in the model outputs. Type III (i.e. partial) Sums of Squares were used for the analysis since they are appropriate for both balanced and unbalanced data, as occurred in our datasets. Assumptions of ANCOVA were assessed using diagnostic plots of model residuals (to check normality, linearity and homoscedascity), and data that did not meet test assumptions were transformed based on values of λ from Box-Cox plots, which is noted in the model output. The addition of a small constant was required to ensure an appropriate transformation when the response variable was zero and, is noted in the model output. Similarly, the covariate (patch size) was $\log_2$ transformed when it improved conformity to test assumptions, reflecting that the span of patch sizes followed a $\log_2$ scale.

The standard process for ANCOVA was followed whereby the saturated model including the interaction term was first tested for homogeneity of slopes, before the unsaturated model without the interaction term was fitted when homogeneity of slopes was upheld. If the saturated model did not show homogeneity of slopes and it was statistically and biologically appropriate, the least homogenous treatment was omitted and the model re-run using the same approach. Regression slope analysis and *t*-tests were also used and are noted in model outputs and test statistics. Assumptions of these tests were assessed using the above approaches. Analyses were conducted using the *MASS* and *car* packages in *R* (v. 3.2.5; *R* Core Team), with alpha at $\alpha = 0.05$. Figures were produced using the *ggplot2* package in *R*, and *Inkscape* (v. 0.91), and for clarity are presented using untransformed response variables and without 95% confidence intervals.

Results

The abiotic environment

Water flow

The mean dissolution of above-canopy clod cards in winter was 40.2 ± 0.6% (± SE, $n = 28$) mass lost, which represents mean environmental flow during the sampling period. The interaction between patch size and kelp density in influencing sub-canopy clod card dissolution was significant (ANCOVA; $F_{(1,24)} = 11.042$, $P = 0.003$). This reflected that while dissolution rates decreased with patch size, the magnitude of the reduction increased with kelp density (Fig. 4.3a). The double density treatment showed the most marked reductions in sub-canopy flow with increasing patch size. Omitting the double density treatment from the model eliminated the significant interaction, and the unsaturated model revealed the significant effect of patch size, but not kelp density (Table 4.2). Regression slope analysis of the zero density treatment (i.e. patches without adult kelp) illustrated that clod cards positioned on the substratum in the sub-canopy position dissolved more slowly with

increasing patch size ($F_{(1,5)}$ = 11.02, P = 0.021). Thus, it appears that during the winter sampling period the reef structures affected the water flow close to their surface as their size increased.

During the spring sampling period, mean dissolution of above-canopy clod cards was 36.9 ± 0.5% (± SE, n = 28) mass lost. This rate, and hence environmental flow, was significantly lower during the spring sampling period than the winter period ($T_{(54)}$ = -4.043, P < 0.001). The overall pattern of sub-canopy flow was the same as in winter (Fig. 4.3b.), and in spring there was a significant interaction between patch size and kelp density affecting the relative dissolution of sub-canopy clod cards (ANCOVA; $F_{(1,24)}$ = 21.405, P < 0.001). Omitting the double density treatment from the model removed the interaction, with the unsaturated model revealing that both patch size and kelp density were significant (Table 4.2). In spring there was no significant relationship between patch size and dissolution of clod cards in the sub-canopy position on the zero density patches ($F_{(1,5)}$ = 5.763, P = 0.062).

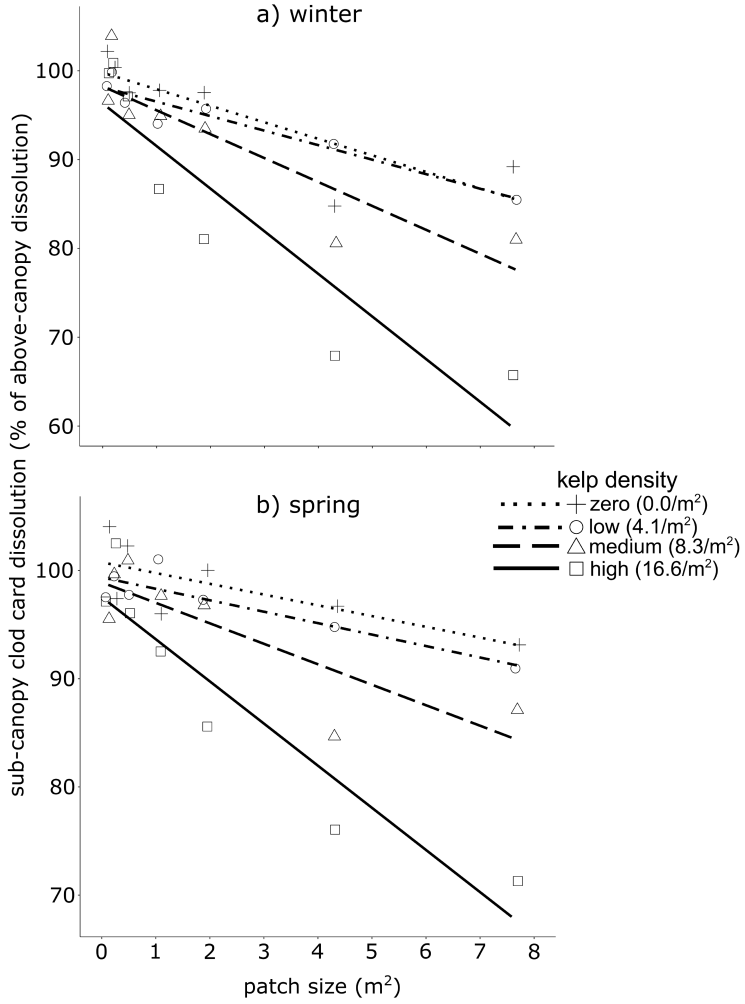

Figure 4.3 Effects of *Ecklonia radiata* patch size and kelp density on sub-canopy water flow, measured as mean dissolution of plaster clod cards relative to the paired above-canopy clod card. Thus 100% represents equal rates of clod card dissolution below and above the kelp canopy, and values higher or lower than 100% indicate greater or less dissolution below the canopy, respectively. Note the different y-axis scales.

Irradiance

Mean above-canopy irradiance during the sampling period was 558 ± 26 µmol photon m^{-2} sec^{-1} (± SE, n = 168) with a maximum of 1417 µmol photon m^{-2} sec^{-1}. Relative sub-canopy irradiance declined with patch size, but only in patches supporting kelp (Fig. 4.4), yielding a significant interaction between patch size and kelp density (Table 4.2). Removing the zero density treatment – for which there was understandably no relationship between 'sub-canopy' irradiance and patch size ($F_{(1,26)}$ = 0.444, P = 0.511) – did not remove the significant interaction, so the original model was retained (Table 4.2).

On treatments with transplanted kelp, relative sub-canopy irradiance decreased dramatically as patch size increased, especially on patches with natural and double densities of kelp (Fig. 4.4). Figure 4.5 illustrates how relative sub-canopy irradiance decreased as kelp density and patch size simultaneously increase, changing from linear decay at smaller patch sizes to negative exponential decay at larger patch sizes. The greatest reduction in irradiance occurred in the largest patch supporting the highest kelp density, where only 1.8 ± 0.3% SE (± SE, n = 6) of above-canopy irradiance reached the sub-canopy (Fig. 4.4). Mean sub-canopy PAR in this patch was 6.2 ± 1.3 µmol photon m^{-2} sec^{-1} (± SE, n = 6).

Table 4.2 Results of ANCOVAs testing effects of kelp density, patch size, and season on abiotic factors below the *Ecklonia radiata* canopy. Output is for either saturated models (where homogeneity of slopes was rejected) or unsaturated models after confirming homogeneity of slopes. Response variable (Y) and associated transformation is noted in the first column. Significant P-values are denoted in bold and with an asterisk.

data analysed	*factor*	*SS (df)*	*F*	*P*
WATER FLOW				
winter (double density omitted) $(Y)^{5.25}$	kelp density	$4.70e^{19}$ (1,18)	2.825	0.110
	$\log_2$(patch size)	$8.58e^{20}$ (1,18)	51.589	**<0.001***
spring (double density omitted) $(Y)^{3.75}$	kelp density	$5.33e^{13}$ (1,18)	6.338	**0.022***
	patch size	$2.54e^{14}$ (1,18)	30.256	**<0.001***
SEDIMENT DEPOSITION				
autumn $(Y)^{0.65}$	kelp density	26.2 (1,24)	2.478	0.128
	patch size	63.9 (1,24)	6.038	**0.022***
winter $(Y)^{-0.15}$	kelp density	0.01 (1,22)	2.557	0.124
	patch size	0.01 (1,22)	5.281	**0.031***
spring $(Y)^{0.60}$	kelp density	204.22 (1,25)	17.384	**<0.001***
	patch size	24.67 (1,25)	2.100	0.160
summer $(Y)^{0.55}$	kelp density	56.71 (1,25)	4.304	**0.048***
	patch size	7.09 (1,25)	0.538	0.470
SEDIMENT ACCUMULATION				
spring (zero density omitted) $(Y+0.1)^{0.60}$	kelp density	1.35 (1,102)	1.480	0.227
	$\log_2$(patch size)	8.39 (1,102)	9.171	**0.003***
summer $(Y+0.1)^{0.35}$	kelp density x $\log_2$(patch size)	2.41 (1,136)	11.560	**<0.001***
IRRADIANCE				
spring $(Y)^{0.15}$	kelp density x $\log_2$(patch size)	0.89 (1,108)	71.120	**<0.001***

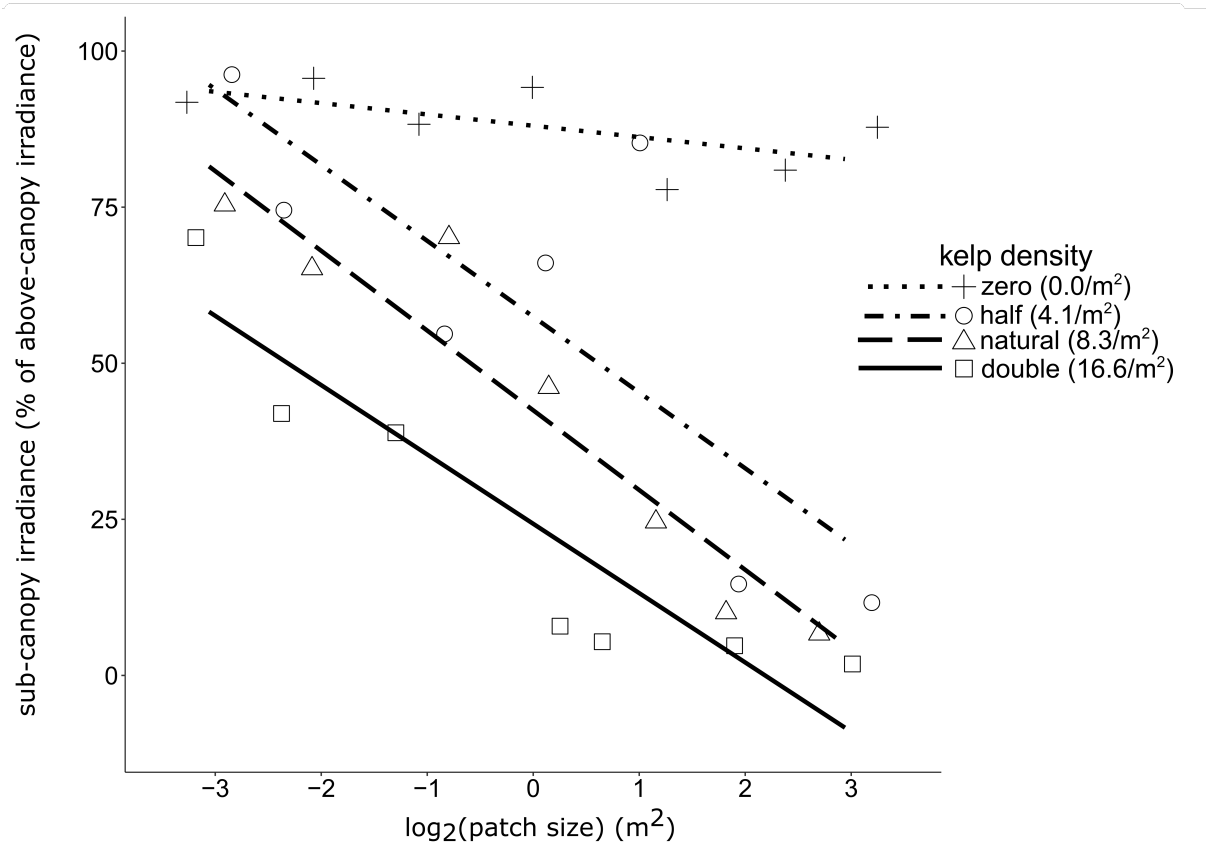

Figure 4.4 Effects of *Ecklonia radiata* patch size and kelp density on sub-canopy irradiance levels, measured as light relative to the paired above-canopy measurement. Thus 100% represents equal light below and above the kelp canopy, and values higher or lower than 100% indicate greater or less light below the canopy, respectively. Mean ambient irradiance was 558 ± 26 µmol photon m^{-2} sec^{-1} (n = 112, ± SE).

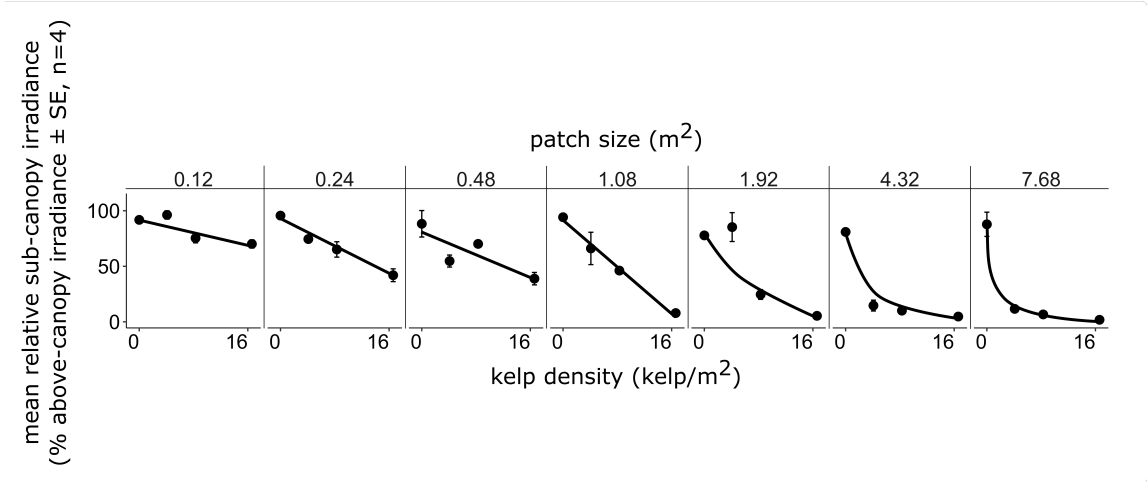

Figure 4.5 Reduction in relative sub-canopy irradiance with increasing density of adult *Ecklonia radiata* shown across all patch sizes. A linear model describing the reduction of light with kelp density is fit to patches ≤1.08 m^2, while nonlinear decay curves are fit to patches ≥1.92 m^2. Light is expressed as a percentage of irradiance measured above the canopy in the same patch.

Sediment deposition

For all seasons except winter, sediment deposition was higher below the kelp canopy than above, with sub-canopy values typically greater than 100% of above canopy rates of deposition (Fig. 4.6). Relative sub-canopy sediment deposition increased significantly with patch size in autumn and winter, but with kelp density in spring and summer (Fig. 4.6, Table 4.2). There was also a clear trend in spring and summer for sub-canopy deposition to increase with patch size on those patches where kelp was present (i.e. half, natural and double density treatments; Fig. 4.6). Above-canopy rates of sediment deposition differed markedly among seasons (autumn, 135.7 ± 7.3 g m^{-2} day^{-1} (± SE, n = 27); winter, 217.0 ± 12.5 g m^{-2} day^{-1} (± SE, n = 25); spring, 28.8 ± 2.1 g m^{-2} day^{-1} (± SE, n = 28); summer, 50.5 ± 3.4 g m^{-2} day^{-1} (± SE, n = 28). The collected sediments were mostly fine to very fine sand (250–62 μm) with some silt (<62 μm). Qualitatively, there were no apparent differences in the sediment composition across seasons.

Sediment accumulation

We never observed unbound or 'free' sediments on the experimental reefs, and sediment particles were always accumulated within algal turfs that consisted of red and green foliose and filamentous algae. These accumulated sediments appeared to be a similar composition to those collected in the sediment traps, being mostly fine sands and some silt.

During spring, sediment accumulation on the reefs ranged from 0–10 mm in depth and there was a significant interaction between patch size and kelp density (ANCOVA; $F_{(1,136)} = 17.601$, $P < 0.001$). In this model, patch size either had a positive relationship (zero density), a negative relationship (natural and double density) or no relationship (half density, $F_{(1,33)} = 0.003$, $P = 0.951$) with sediment accumulation (Fig. 4.7a). Omitting the zero density treatment from the model removed the significant interaction, and in this case, the unsaturated model illustrated that as patch size increased sediment accumulation decreased (Table 4.2).

During summer, sediment accumulation ranged between 0–11 mm in depth and, as in spring, there was a significant interaction between patch size and kelp density (Fig. 4.7b, Table 4.2). This reflected that sediment accumulation was similar across patch sizes in the zero density treatment (Fig. 4.7b, $F_{(1,33)} = 3.65$, $P = 0.065$), but declined (marginally) with patch size in half density treatment ($F_{(1,33)} = 1.182$, $P = 0.049$). The decline in sediment accumulation with patch size was even more marked at natural and double density. No appropriate term could be omitted from the saturated model to remove the significant interaction, and so it was not possible to analyse main effects.

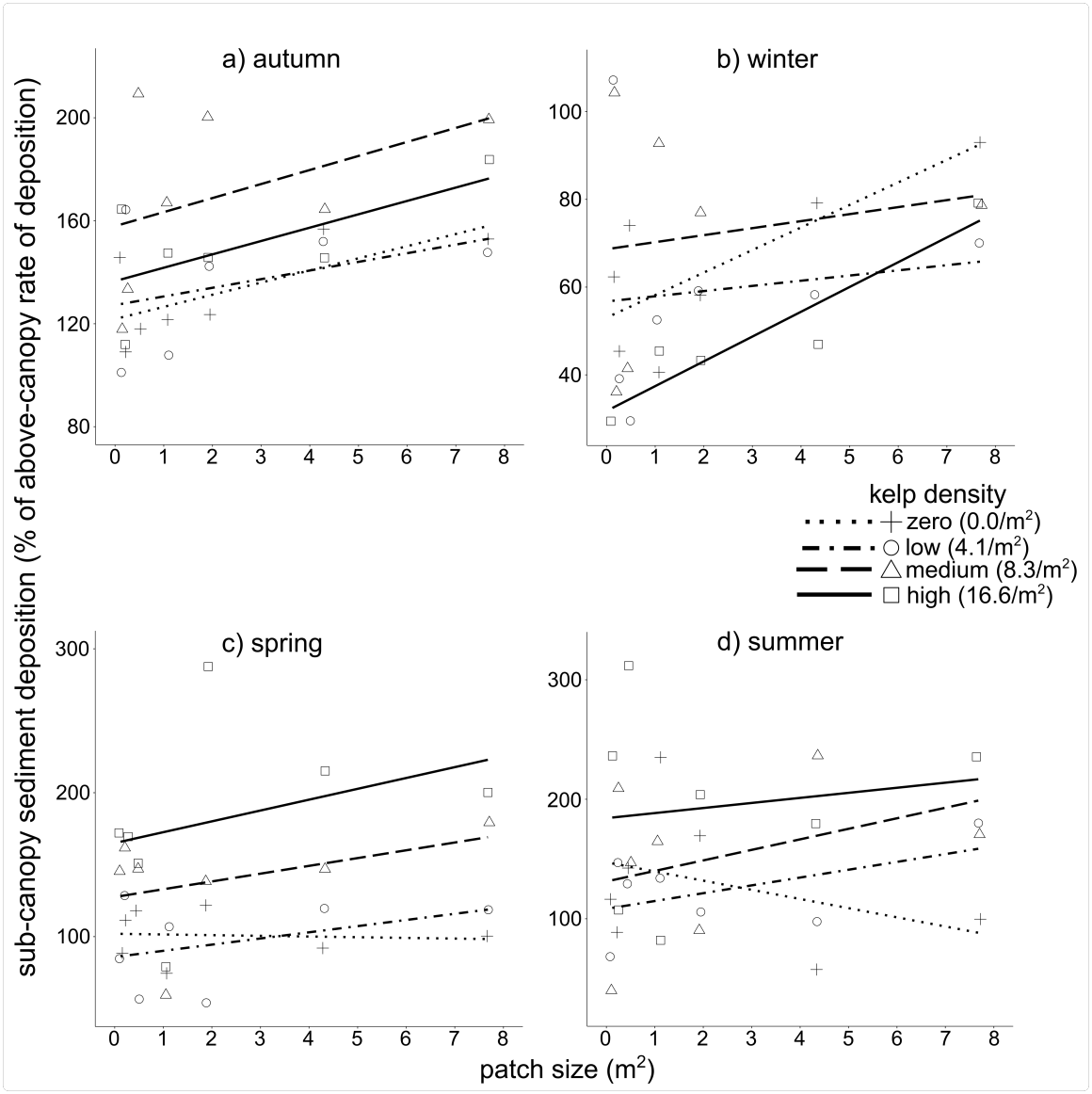

Figure 4.6 Effects of *Ecklonia radiata* patch size and kelp density on sub-canopy sediment deposition. Data are expressed as percentage of sediment deposition relative to the deposition recorded in a paired sediment trap above the canopy. Thus 100% represents equal rates of deposition below and above the kelp canopy, and values higher or lower than 100% indicate greater or less deposition below the canopy, respectively. Note the different y-axis scales.

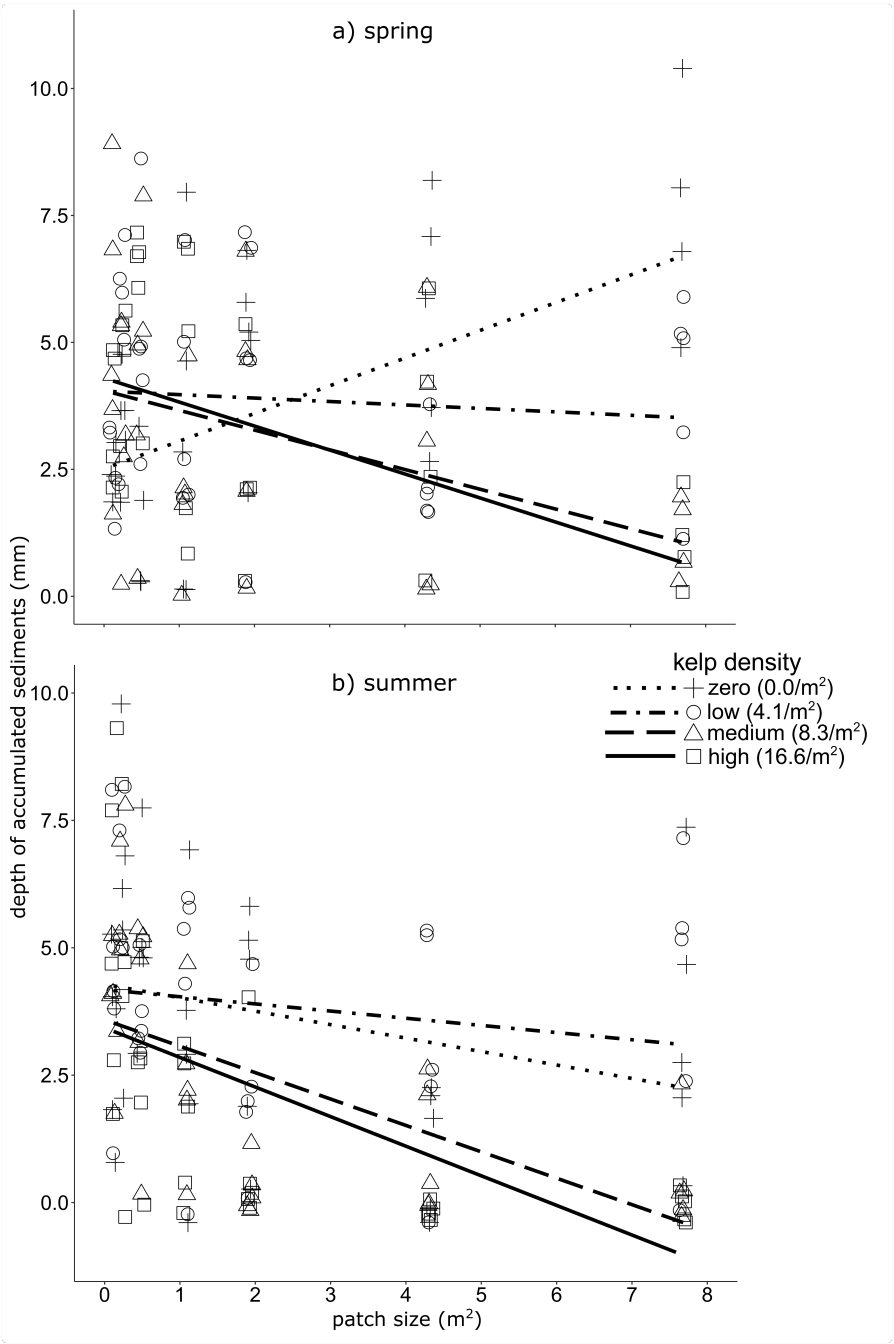

Figure 4.7 Effects of *Ecklonia radiata* patch size and kelp density on the depth (mm) of accumulated sediments in turf-sediment matrices growing on the reef substratum.

Kelp demographics

Survivorship of transplanted macroscopic juvenile sporophytes

During autumn, survivorship of juveniles transplanted into patches of natural kelp density increased significantly with increasing patch size (Table 4.3). After 90 days, there were no surviving juveniles on the two smallest patches (<0.25 m^2), with survivorship appeared to stabilise in patches larger than 1 m^2, where it was ≥80% in each patch (Fig. 4.8).

During spring and summer – when juveniles were transplanted across a subset of patch sizes but across all four kelp density treatments (Table 4.1) – there was significantly higher survivorship with increasing patch sizes, and in spring than summer (Table 4.3). Kelp density did not have a significant effect on survivorship (Table 4.3), although juveniles transplanted into patches of zero kelp density typically had the poorest survivorship: especially in summer when no juveniles survived on any patches without adult kelp (Fig. 4.8). Juvenile sporophytes transplanted to patches of natural density tended to have the highest survivorship, while those on half and double density patches showed intermediate survivorship.

For juveniles transplanted into patches of natural density, there was a significant interaction between season and patch size (ANCOVA; $F_{(2,11)} = 4.749$, $P = 0.033$). Omitting the data from spring, when juveniles displayed far higher survivorship (Fig. 4.8), eliminated the significant interaction and revealed that survivorship increased with patch size, but did not differ between autumn and summer (Table 4.3).

Growth of transplanted juvenile sporophytes

The growth of juvenile sporophytes transplanted into patches of natural density increased with patch size and differed across seasons (Fig.4.9, Table 4.3). Juveniles transplanted during autumn had significantly higher growth rates than in other seasons. Using the juveniles transplanted into the largest patch as a reference – since they showed the highest growth rates – mean seasonal growth rates were 19.4 ± 1.4 mm/week (± SE, $n = 10$) in autumn, 11.4 ± 1.8 mm/week (± SE, $n = 9$) in spring and 10.1 ± 1.3 mm/week (± SE, $n = 10$) in summer.

Because no juveniles transplanted into patches without adult kelp survived over summer, testing for differences in growth rates across kelp density treatments and patch size was limited to spring (Fig. 4.10). For those juvenile sporophytes, growth rates increased significantly with patch size, but not kelp density (Table 4.3). However, this effect was evident only for juveniles transplanted into patches of half and natural kelp density, and regression slope analysis indicated no relationship between growth rates and patch size in the zero ($F_{(1,15)} = 1.056$, $P = 0.321$) and double density treatments ($F_{(1,19)} = 1.028$, $P = 0.323$).

Density x patch size x season effects on growth were tested by examining those juveniles transplanted during spring and summer onto patches supporting adult kelp. Growth rates of these individuals increased significantly with patch size but not kelp density (although here $P = 0.059$), with higher growth rates in spring than summer (Fig. 4.11, Table 4.3). Growth rates of juveniles transplanted into patches of double kelp density were not however influenced by patch size during spring ($F_{(1,19)} = 1.028$, $P = 0.323$) or summer ($F_{(1,7)} = 0.248$, $P = 0.634$).

Table 4.3 Results of ANCOVAs (and one linear regression[1]) testing effects of kelp density, patch size, and season on early life history stages of *Ecklonia radiata*. ANCOVA output is for unsaturated models after confirming homogeneity of slopes. Response variable (Y) and associated transformation is noted in the first column. Significant P-values are denoted in bold and with an asterisk.

data analysed	*factor*	*SS (df)*	*F*	*P*
SURVIVORSHIP OF TRANSPLANTED JUVENILE SPOROPHYTES				
autumn[1] $(Y+0.1)^{0.50}$	$\log_2$(patch size)	82.68 (1,4)	12.306	**0.017***
spring + summer $(Y+0.1)^{0.70}$	season	293.85 (1,23)	7.227	**0.013***
	kelp density	17.89 (1,23)	0.440	0.514
	$\log_2$(patch size)	218.09 (1,23)	5.364	**0.030***
natural density (spring omitted) $(Y+0.1)^{0.70}$	season	3.08 (1,9)	0.101	0.758
	$\log_2$(patch size)	814.77 (1,9)	26.589	**<0.001***
GROWTH OF TRANSPLANTED JUVENILE SPOROPHYTES				
natural density $(Y)^{0.60}$	season	56.68 (2,110)	41.568	**<0.001***
	patch size	9.53 (1,110)	13.977	**<0.001***
spring $(Y)^{0.40}$	kelp density	0.07 (1,89)	0.706	0.403
	patch size	0.64 (1,88)	6.719	**0.011***
spring + summer $(Y)^{0.55}$	season	3.05 (1,131)	6.933	**0.009***
	kelp density	1.60 (1,131)	3.641	0.059
	patch size	5.86 (1,131)	13.334	**<0.001***
MICROSCOPIC SPOROPHYTES				
recruitment (zero density omitted) $(Y+0.01)^{-0.65}$	kelp density	98.35 (1,18)	2.729	0.116
	$\log_2$(patch size)	689.26 (1,18)	19.123	**<0.001***
survivorship (zero density omitted) $(Y+0.01)^{-0.15}$	kelp density	0.06 (1,18)	1.084	0.312
	$\log_2$(patch size)	4.31 (1,18)	77.546	**<0.001***
RECRUITMENT OF MACROSCOPIC JUVENILE SPOROPHYTES				
spring $(Y)^{-0.45}$	kelp density	1.40 (1,11)	3.121	0.105
	$\log_2$(patch size)	6.03 (1,11)	13.440	**0.004***
winter $(Y)^{-0.40}$	kelp density	2.44 (1,11)	7.214	**0.021***
	$\log_2$(patch size)	5.33 (1,11)	15.766	**0.002***
end of study (November 2016) $(Y)^{-0.2}$	kelp density	0.19 (1,18)	3.999	0.061
	$\log_2$(patch size)	2.51 (1,18)	52.693	**<0.001***

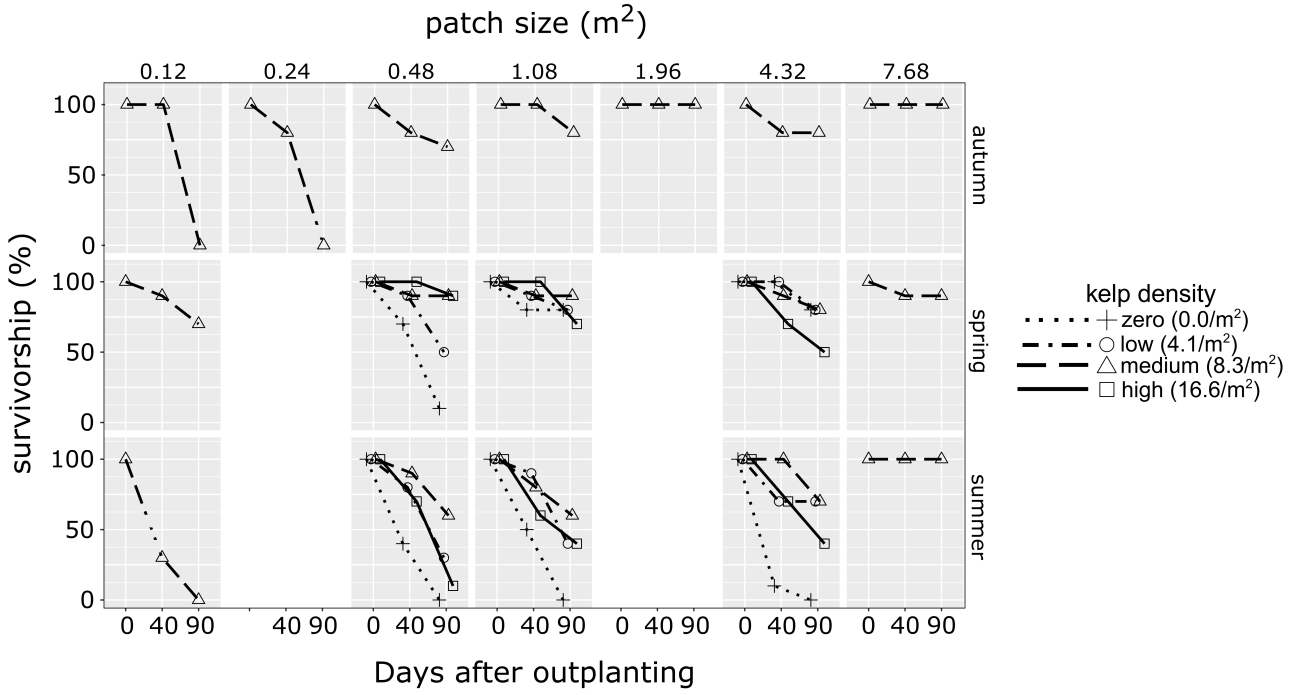

Figure 4.8 Survivorship curves of transplanted stage 1 juvenile *Ecklonia radiata* sporophytes showing differences with patch size, season, and kelp density.

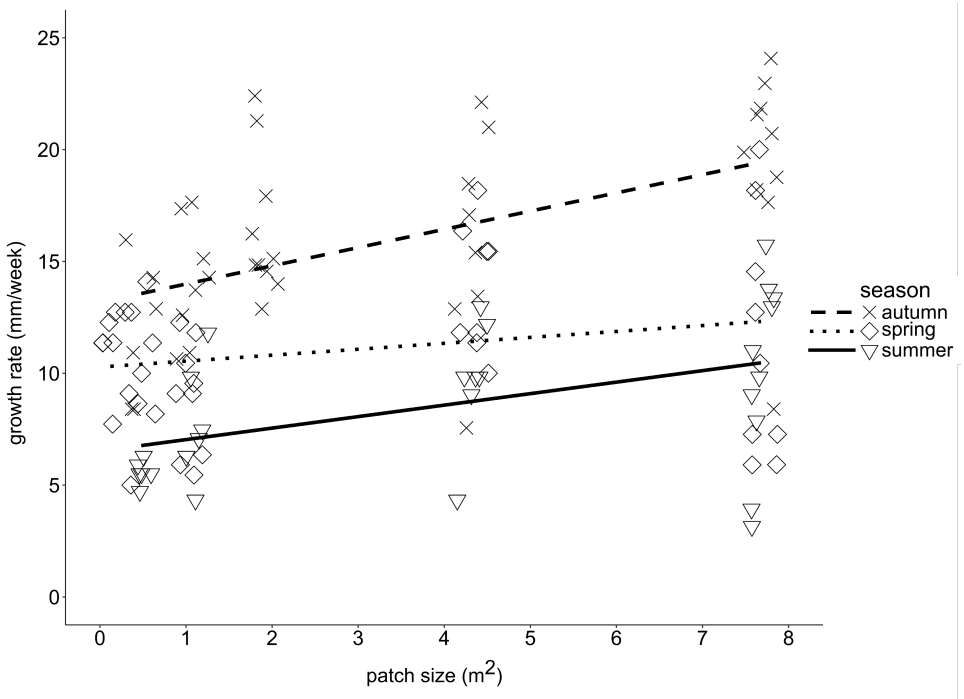

Figure 4.9 Growth rate of macroscopic juvenile *Ecklonia radiata* sporophytes dependent on patch size 90 days after being transplanted into patches at natural kelp density (8.3 kelp/m^2).

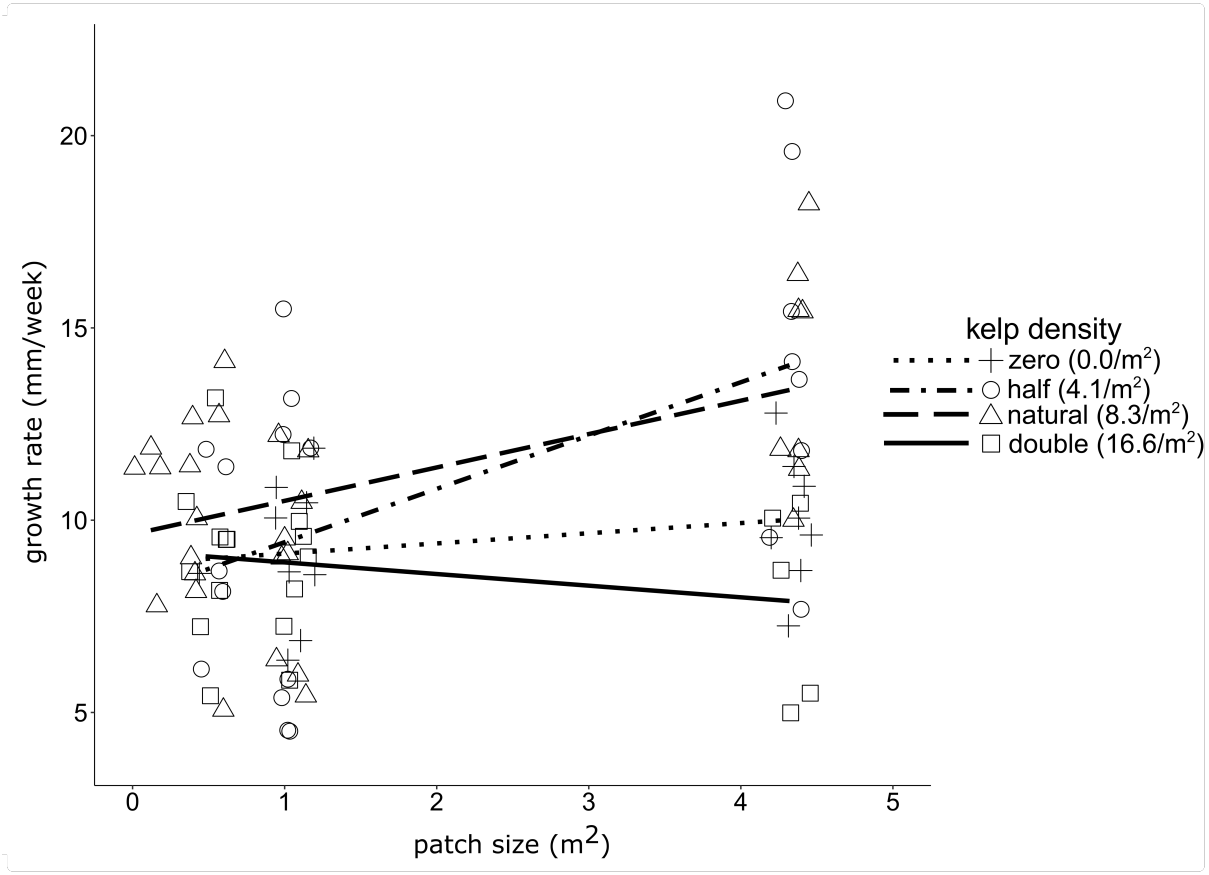

Figure 4.10 Growth rate of macroscopic juvenile *Ecklonia radiata* sporophytes dependent on patch size, 90 days after being transplanted to patches of varying kelp density during spring.

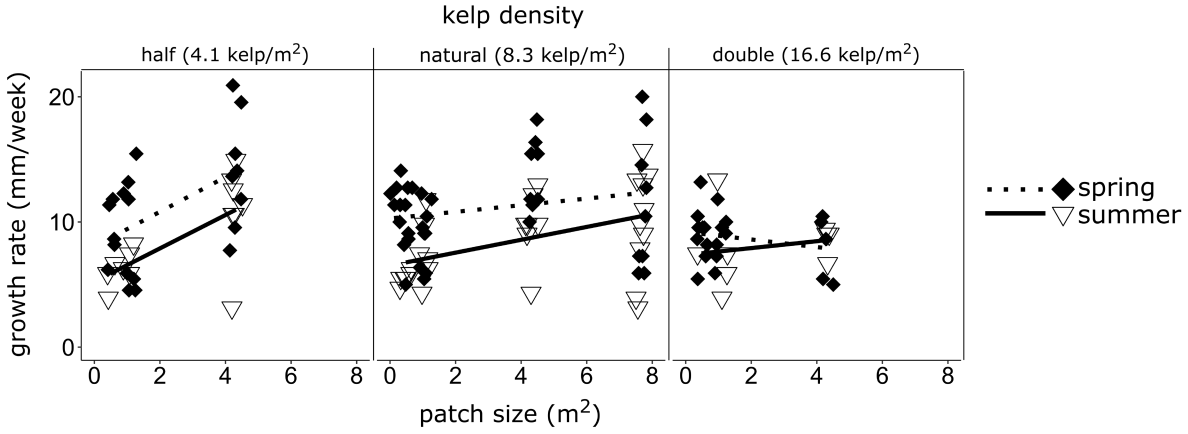

Figure 4.11 Growth rate of macroscopic juvenile *Ecklonia radiata* sporophytes dependent on patch size, 90 days after being transplanted to patches of varying kelp density during spring and summer.

Recruitment and survivorship of microscopic sporophytes

After the 42-day outplanting period, only 19 naturally recruited microscopic sporophytes were observed on the blank control slides. Recruitment of microscopic sporophytes was greatest in the largest patch supporting the highest kelp density, while none occurred on patches <1.92 m^2 (regardless of kelp density) nor on any patches without adult kelp (Fig. 4.12a). There was a significant interaction between patch size and kelp density (ANCOVA; $F_{(1,24)} = 9.523$, $P < 0.005$), likely reflecting the absence of recruitment on the zero density treatment. Indeed, after omitting the zero density plots the significant interaction was removed, and recruitment increased significantly with patch size, but not kelp density (Table 4.3).

Survivorship of the outplanted microscopic sporophytes was also low, and only 353 of the ~2,500,000 outplanted sporophytes survived. The largest patch supporting the highest kelp density had by far the most surviving sporophytes, where 200 individuals remained after the outplanting period, but no microscopic sporophytes survived on any reefs <1 m^2 (regardless of kelp density) nor on any patches without adult kelp (Fig. 4.12b). Again, a significant interaction between patch size and kelp density (ANCOVA; $F_{(1,24)} = 9.740$, $P < 0.005$) disappeared following omission of the zero density treatment. Subsequently, the unsaturated model illustrated that survivorship of outplanted microscopic sporophytes increased significantly with patch size, but not kelp density (Table 4.3).

Recruitment of macroscopic juvenile sporophytes

Macroscopic recruits first appeared in early spring (September) ~7 months after the initial transplanting of adult kelp and occurred on the largest patch supporting the highest density of adult kelp. It was another 2 months until macroscopic recruits were observed on any other patches.

Throughout the experiment, no recruits were observed on any of reefs devoid of adult kelp. Recruits were sporadically observed on some reefs from the half kelp density treatment, and while none were recorded during the initial two censuses, sampling at the end of the study revealed some recruits on these patches (Fig. 4.13). Only a single recruit was ever observed on reefs smaller than 1 m^2 throughout the whole experiment. During each census, the density of juvenile recruits was found to increase significantly with patch size (Table 4.3). The density of recruits only increased significantly with adult kelp density during the winter census. However, during the other two censuses, there was a trend for patches supporting kelp at double density to have a greater absolute number of recruits and at higher densities, with the largest number of recruits each period occurring on the largest reef supporting the highest density of adult kelp (Fig. 4.13).

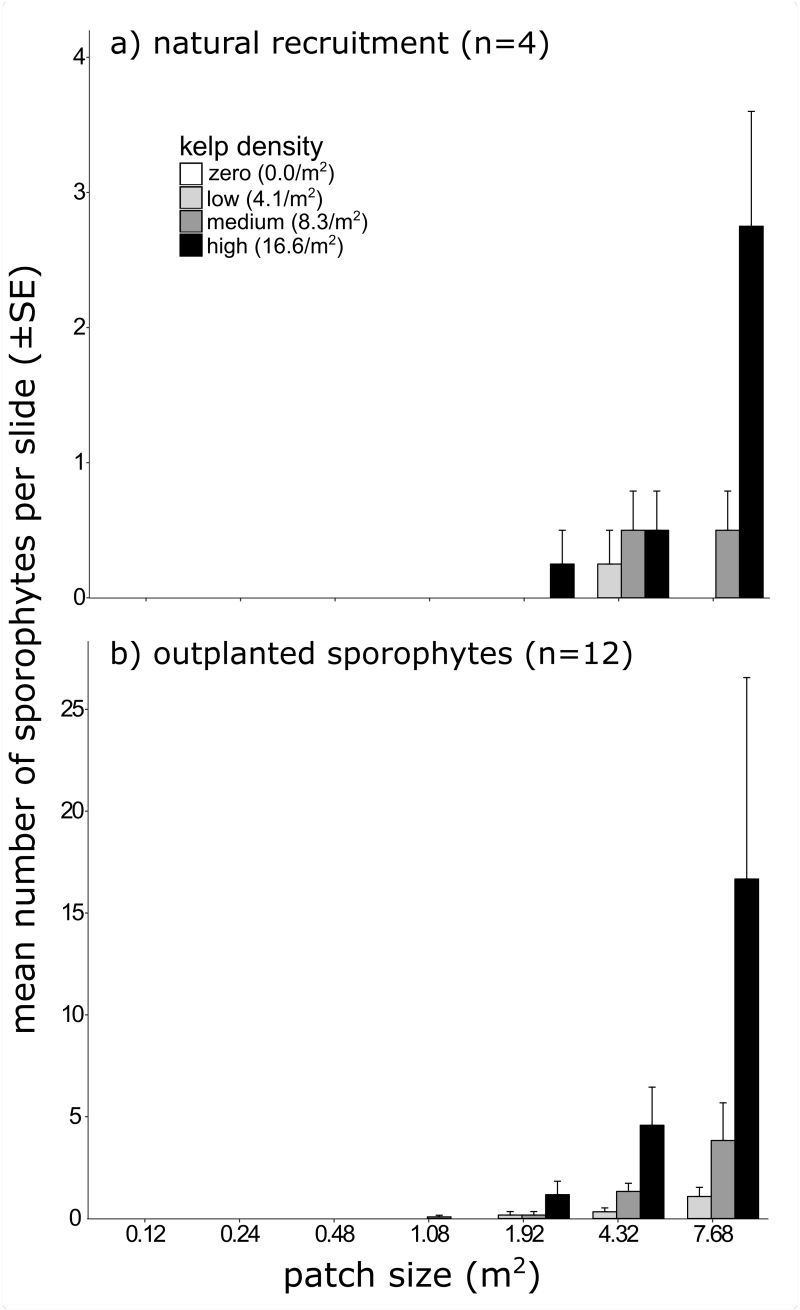

Figure 4.12 (a) Mean number (± SE) of (a) naturally recruited microscopic *Ecklonia radiata* sporophytes, dependent on patch size and kelp density on blank slides; and (b) mean number of surviving microscopic sporophytes grown on slides 42 days after outplanting, dependent on patch size and kelp density. Note the different y-axis scales, and that the data on patch size 1.08 m^2 (Fig. b) is from the natural density treatment.

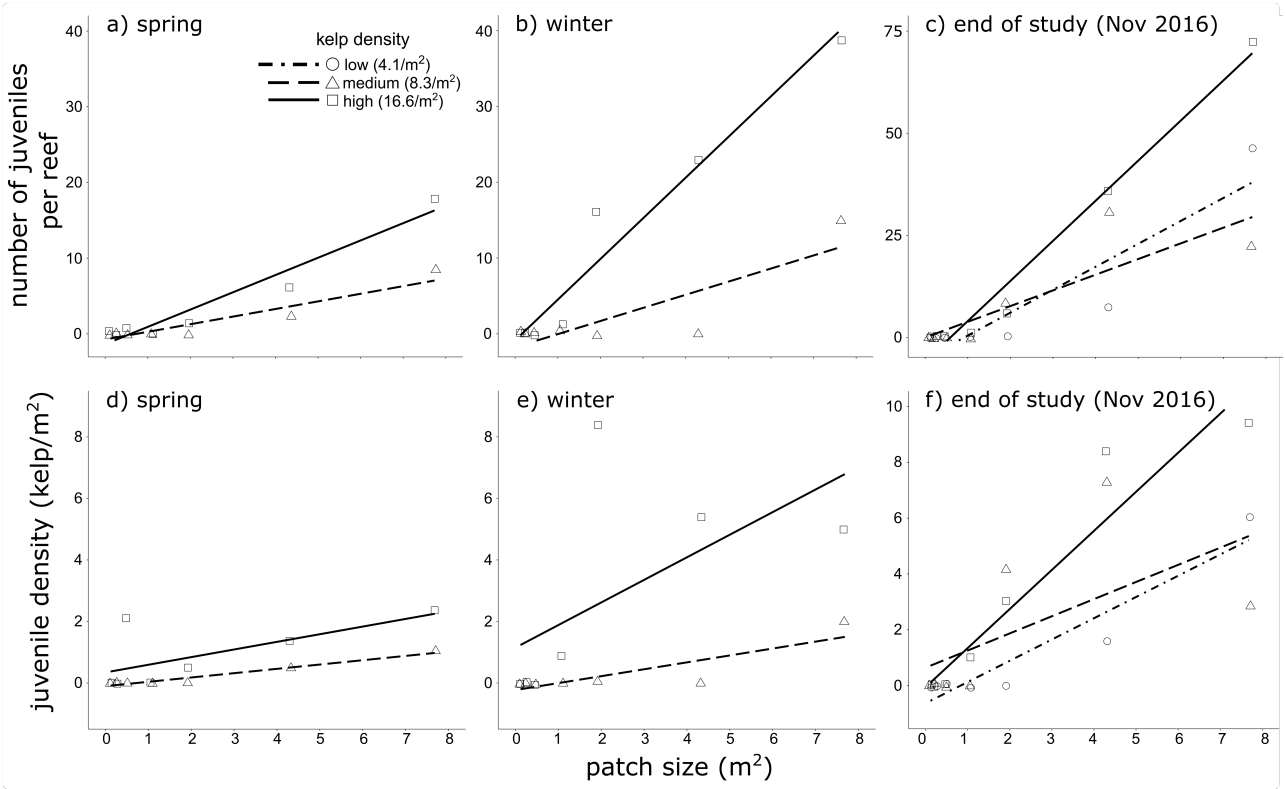

Figure 4.13 Recruitment of macroscopic juvenile *Ecklonia radiata* sporophytes on different sized patch reefs at half (end of study only), natural and double kelp density, censused during spring, winter and at the end of the study (November 2016). Expressed as (a,b,c) absolute number of juveniles per patch and (d,e,f) density of recruits (no. individuals/m^2). Tests were only conducted on density of recruits. Note the different y-axis scales.

Discussion

Ecosystem engineering by canopies of *Ecklonia radiata* modifies the physical environment to reduce water flow, sedimentation and irradiance within the sub-canopy. However, the capacity of this kelp to engineer abiotic change is largely dependent on patch size, and to a lesser extent, adult kelp density. Moreover, the recruitment, growth and survivorship of microscopic and macroscopic juvenile *E. radiata* are all impaired by reductions in patch size and kelp density. Even after the provision of established propagules and juvenile sporophytes, many of these demographic processes collapsed in the absence of sufficient adult kelp.

Ecosystem engineering of the abiotic environment

Water flow

Patch size was the most important factor affecting water flow below the *E. radiata* canopy on the experimental reefs, with larger patches having lower sub-canopy flows. However, this effect was diminished as patch size decreased, and patches <1 m^2 (and regardless of kelp density) showed a limited capacity to modify flow (Fig. 4.3).

We recorded sub-canopy water flow as low as 66% and 71% of above-canopy flows, during winter and spring respectively (Fig. 4.3). Eckman et al. (1989) installed plaster clod cards beneath a mixed kelp canopy of *Agarum* spp. and *Laminaria saccharina* at depths between 7–11 m and demonstrated that flow was 42–50% of that external to the canopy. This is the only published measure of flow beneath a stipitate kelp of which we are aware. Whilst our observations of sub-canopy flow were not as low, our experimental kelp patches were smaller than the natural habitats investigated by Eckman and co-authors. Accordingly, the capacity of natural stands of *E. radiata* to reduce environmental water flow may be even greater than our results indicate. Water flow is highly variable across space and time, and we acknowledge that differences in site-exposure, season and weather conditions may equally explain the disparity between the results.

The strong effect of patch size in modifying sub-canopy flow compared to the weaker and more seasonal effect of kelp density suggests that water entering through the sides of *E. radiata* patches, rather than through the canopy, plays a large part in determining sub-canopy hydrodynamics. The work by Eckman et al. (1989) demonstrates that tracer particle penetration through the kelp canopy (and thus mass transfer and water flow) is minimal and supports this interpretation. It follows that the mechanisms responsible for reducing sub-canopy flow are likely the baffling effect of the stipes along with friction on the benthos and underside of the kelp canopy (Fonseca & Fisher 1986; Denny et al. 1998). We suggest that the stipes, and possibly even the holdfasts, of *E. radiata* may be as important as the kelp canopy in modifying sub-canopy hydrodynamics.

Kelp density only significantly affected sub-canopy flow during spring. The trend for sub-canopy flow to decrease with increasing kelp density was also evident during winter but not significant (Table 4.2). Given the capacity of the different kelp densities to modify flow was most pronounced in the largest patches, kelp density may be a more important factor in the modification of flow in kelp patches beyond the size of our experimental reefs.

The inconsistent effect of kelp density on flow between winter and spring is likely to reflect seasonal differences in canopy biomass, which for *E. radiata* is typically highest in spring and early summer and lowest in autumn and early winter (Larkum 1986; Fairhead & Cheshire 2004). Thus, increased biomass in spring may have amplified the canopy's ability to modify flow.

Ambient water flow was significantly higher during the winter sampling period than in spring, reflecting seasonality in storm events and sea conditions. Whether this is responsible for the seasonal differences in kelp density effects is unclear. Also, during winter the reef structures themselves appeared to affect flow, evident by significant reductions in 'sub-canopy' flow on reefs without adult kelp. The reef structures (especially those >4 m^2) may have moderated intense winter conditions – possibly via the formation of eddies (Porter et al. 2000) – sufficiently to detect an effect.

Any artefact from the reef structures is unlikely to have influenced the broader results however, given the reductions in flow were slight relative to those observed on reefs with adult kelp (Fig. 4.3).

Ultimately, the degradation of *E. radiata* habitats through reductions in patch size and kelp density seems to increase sub-canopy water flow in these environments. This has the potential to influence a suite of physiological dynamics (reviewed by Hurd 2000) and other abiotic factors including kelp scour (Fletcher & Day 1983; Kennelly 1989) and sedimentation (Eckman et al. 1989; Connell 2003).

Light

The light regime in kelp forests strongly influences the associated community (Wernberg et al. 2005; Flukes et al. 2014), the kelp itself (Wood 1987) and indirectly, other abiotic factors such as sedimentation (Kennelly 1987b). The ability of *E. radiata* and other stipitate kelp to modify sub-canopy irradiance is well recognised (Dayton et al. 1984; Kennelly 1989; Wernberg et al. 2005; Schiel & Foster 2006). Although we demonstrate that the capacity of *E. radiata* to regulate sub-canopy light alters dramatically as patch size and kelp density is reduced (Fig. 4.4).

The largest patch supporting the densest kelp showed the greatest capacity to modify light, and sub-canopy irradiance on this reef was ~6 µmol photon m^{-2} sec^{-1} (~2% of above canopy levels). This is similar to previously reported measurements of irradiance beneath *E. radiata* canopies at similar depths (7–9 µmol photon m^{-2} sec^{-1}, Kennelly 1989; ~10 µmol photon m^{-2} sec^{-1}, Wernberg et al. 2005), although these studies used flat PAR sensors. Along with patch size, kelp density also plays an important role in shaping sub-canopy light conditions and the two factors interact (Fig. 4.4, Table 4.2). Wernberg et al. (2005) illustrated similar effects of kelp density on sub-canopy light within a natural stand of *E. radiata*.

The exponential changes to sub-canopy irradiance we observed (Fig. 4.5) largely seems due to the importance of patch size in minimising the incidental irradiance that enters through the sides of patches. Despite the sparse canopy, the largest patch supporting kelp at half-natural density had relatively low light levels, with only ~15% of above-canopy light reaching the benthos. In contrast, in smaller patches supporting kelp at natural and double-natural density, 50–75% of above-canopy light penetrated to the sub-canopy (279–419 µmol photon m^{-2} sec^{-1}). Irradiance entering from the sides of the patches must therefore comprise a substantial portion of the light that reaches the sub-canopy environment. Thus, previous measurements of light using flat sensors are likely to have underestimated sub-canopy irradiance, especially in smaller patches.

Small and lower density patches are also likely to have more variable sub-canopy light environments due to the interrelation between water flow, canopy movement and light flecking

(Toohey & Kendrick 2008; Raven & Hurd 2012). Due to the short period of our measurements, we were unable to fully illustrate the temporal variability in sub-canopy light conditions.

Our results suggest that large and/or dense areas of *E. radiata* may possess a buffering capacity to moderate sub-canopy light in spite of some level of habitat degradation. We emphasise however that reductions to either patch size or kelp density, even when small, in habitats that have already experienced habitat degradation can result in dramatic increases in sub-canopy irradiance. This is likely to have significant implications for not only the understorey community, but also the juvenile life-stages of *E. radiata* that develop beneath the adult canopy.

Sediment deposition

It is well established that *E. radiata* can modify sub-canopy sedimentation (Connell 2003; Wernberg et al. 2005; Toohey et al. 2007). Here we show that the deposition of sediments beneath the canopy of *E. radiata* typically increase with the separate effects patch size and density of the kelp patches (Fig. 4.6, Table 4.2).

Sediment deposition within a kelp forest is a function of the supply of sediment particles available for deposition, water flow and settling velocities of the particles, and the ability of the kelp canopy to intercept particles (Komar & Miller 1973; Eckman et al. 1989; Airoldi 2003; Connell 2003). The supply of sediment particles for deposition on the experimental patches likely originated from resuspended local sediments (Komar & Miller 1973), since there are no riverine inputs in the area. Small-scale hydrodynamic processes – especially the reduction of sub-canopy flow – were then likely responsible for particle settling into the sub-canopy (Fonseca & Fisher 1986; Jürg 1996). Our data on sub-canopy flow (Fig. 4.3) supports this explanation, and the highest rates of deposition typically occurred in patches with the lowest sub-canopy flows.

Interactions between environmental and physical processes meant that sediment deposition across the site was variable and highly seasonal. For example, rates of sediment deposition during winter (the season of highest deposition) were over 7 times greater than in spring, when deposition rates were lowest. The precise cause behind this is unclear; however, it was likely caused by seasonal differences in suspended sediment loads, possibly due to winter storms (Komar & Miller 1973; pers. obs.). Further, while patch size but not kelp density significantly affected sediment deposition during autumn and winter, the opposite held during spring and summer. The significance of kelp density in influencing sediment deposition during spring is consistent with seasonal variations in canopy biomass influencing the extent of ecosystem engineering by *E. radiata.* Overall, it seems that both patch size and *E. radiata* density can affect sediment deposition under certain conditions.

We conclude that degradation of *E. radiata* stands may in fact reduce sub-canopy sediment deposition; however, the magnitude of the impact is likely to be highly dependent on local

environmental dynamics. Nonetheless, the benthos in natural and intact *E. radiata* stands is typically characterised by a distinct absence of sediments (Kennelly 1987a; Airoldi 2003; Toohey et al. 2004), and this is because sedimentation is a two-part process involving not only deposition, but also accumulation.

Sediment accumulation

The turf algae-sediment matrix that developed on the experimental reefs is typical of sedimentation on rocky reefs elsewhere in Australia (Kennelly 1987b; Valentine & Johnson 2005) and around the world (Airoldi 2003; Strain et al. 2014). The negative effects of this kind of sedimentation on reef ecosystems worldwide is well documented (see reviews Airoldi 2003, Strain et al. 2014). Our results complement existing work (Kennelly 1989; Connell 2003; Wernberg et al. 2005) illustrating that ecosystem engineering by *E. radiata* strongly modifies sub-canopy sediments, with the depth of sediments on our experimental reefs approaching zero with increasing patch size and kelp density (Fig. 4.7). This resulted in the paradoxical situation where the least sediment accumulation occurred on reefs with the highest rates of sediment deposition.

Patch size was the main factor affecting sediment accumulation on the experimental reefs and during both spring and summer, sediment accumulation increased as patch size decreased. This was likely influenced by the higher sub-canopy irradiances we observed on the smaller patches, which stimulates the formation of the sediment-capturing turf algae (Kennelly 1989; Connell 2003). Although, despite exhibiting similar levels of sub-canopy irradiance, some patches of the same size but supporting a different density of kelp had markedly different amounts of accumulated sediments. This was especially noticeable for the two largest patch sizes (Figs. 4.4, 4.7).

Observations from summer revealed that increasing kelp density and patch size interact to reduce sediment accumulation (with a similar but not significant trend evident in spring). Wernberg et al. (2005) also observed that sub-canopy sediment cover decreases with increasing density of *E. radiata*. Thus, the density of *E. radiata* is an important factor shaping sediment accumulation under certain circumstances, possibly due to scouring of the benthos by the kelp lamina. Kelp scour not only suppresses the development of algal turfs (Kendrick 1991, Connell 2003; Irving & Connell 2006), and thus indirectly limits sediment accumulation, but also physically removes sediments via sweeping of the kelp lamina (Kennelly 1989). Exactly how and why kelp density effects vary with season is unclear, however, seasonal fluctuations in canopy biomass and water flow (which is tightly related to kelp scour, see Fletcher & Day 1983; Kennelly 1989) may explain this.

Natural and double density treatments had an almost exponential increase in sediment accumulation with decreasing patch size, compared to reefs with half and zero densities of kelp. This is concerning given the negative effects that sediments have on the colonising life stages of *E. radiata* and other kelp species (Devinny & Volse 1978; Kennelly 1987b; Airoldi 2003). These types of

nonlinear 'tipping-point' responses are of particular interest given that productive kelp ecosystems can rapidly phase shift to denuded turf algae-sediment habitats (Airoldi 2003; Connell et al. 2008; Strain et al. 2014).

Interactions between sediment deposition, irradiance, scour, and turf algae (see also Wernberg et al. 2005; Irving & Connell 2006) resulted in the most sediment accumulation occurring on those reefs with the least deposition (and vice versa). This 'sediment paradox' suggests that sedimentation within *E. radiata*-dominated ecosystems is driven primarily by factors that regulate the capture and accumulation of sediments rather than their supply and deposition. Accordingly, it seems the accumulation of sediments within algal turfs – which are promoted by increased light and reduced kelp scour – are likely to increase within degraded *E. radiata* stands.

Kelp demographics

Survivorship of transplanted macroscopic juveniles

Survival of the transplanted macroscopic juvenile sporophytes varied widely, but typically increased with patch size (Table 4.3). There were no significant effects of kelp density on the survival of the juvenile sporophytes. However, juveniles transplanted onto patches without any adult kelp tended to have very poor survivorship, while those from the natural density treatments fared best (Fig. 4.8).

Juvenile *E. radiata* are adapted to persist in the low-light conditions typically present beneath intact canopies of adult conspecifics (Wood 1987; Kirkman 1981; Toohey & Kendrick 2007). In fact, small juvenile *E. radiata* – in addition to some species of red algae – are often the only macroalgae that occur beneath dense adult canopies (Wernberg et al. 2005; pers. obs). Thus, the patterns of survivorship we observed may largely be attributed to irradiance, which we show is strongly influenced by patch size and kelp density.

Canopy removal experiments have demonstrated that juvenile *E. radiata* can experience pigment loss, tissue necrosis and increased mortality when exposed to elevated irradiances (~720 μmol photon m^{-2} sec^{-1} *sensu* Wood 1987; Toohey & Kendrick 2007). Certainly, those authors' descriptions of juvenile *E. radiata* with bleached holdfasts and eroded lamina or stipes, mirror our own observations. Wood (1987) also illustrated that high-light stress increases as adult kelp density decreases. Notably, photoacclimation and/or phenotypic plasticity may enable juvenile kelp that develop within the brighter sub-canopy of small patches – relative to transplanted individuals – to be more tolerant of increased irradiance (Toohey et al. 2004, Toohey & Kendrick 2007). Thus, the findings of high-light stress by Wood (1987) and Toohey & Kendrick (2007) may be more indicative of the response of juvenile kelp to a pulse disturbance of the canopy (e.g. due to a storm) rather than a press disturbance (e.g. habitat fragmentation). No less, we suggest that exposure to increased sub-

canopy irradiance is likely to have contributed to the poor survivorship of the juvenile sporophytes from the smaller reefs and zero and half density treatments.

Elevated irradiance cannot explain the trend of intermediate survival that we observed on patches from the double kelp density treatment. In those instances, survivorship may instead be shaped by inadequate light. Our readings of minimum sub-canopy irradiance, recorded within the two largest reefs from the double density treatment, were very close to the point of photosynthetic compensation for Laminarians (Lüning & Dring 1979). As such, the quantity of light within patches of double kelp density may have at times been insufficient for photosynthesis. Yet, stage 1 juvenile *E. radiata* are known to retard their development for extended periods (>90 days) in response to sub-optimal sub-canopy conditions (Kirkman 1981; Toohey & Kendrick 2007). Therefore, even if light was insufficient for photosynthesis in the double density treatment, it is unclear whether it would lead to the mortality of the transplanted juveniles. Responses of juvenile *E. radiata* to varying levels of irradiance and their photoacclimative ability, are promising avenues for future research.

Other abiotic factors may amplify the effects of deleterious irradiance (whether too much or too little). For example, elevated water flow can cause abrasion and erosion of *E. radiata* sporophytes (Eckman et al. 1989), which may exacerbate the tissue necrosis caused by high light stress. Our observations of increased water flow in the zero and half density treatments, and the smaller patches, are consistent with this notion.

Herbivory is unlikely to have affected the survivorship of the transplanted juveniles, and while mesograzers such as the small gastropod *Phasianotrochus* spp. were recorded on the reefs (but not at high abundances) we never observed any herbivory nor signs of grazing. Moreover, *Olisthops cyanomelas* – the primary fish species consumes *E. radiata* (Jones & Andrew 1990) – was never observed during fish surveys and is only sporadically distributed in southern Tasmania, and only one small sea urchin (*Heliocidaris erythrogramma*) was ever recorded (Shelamoff et al. in prep.).

There were significant seasonal differences in survivorship, driven primarily by the consistently higher levels of survivorship observed throughout spring. Seasonal variations in canopy biomass and shading may provide some explanation of these results. However, that cannot explain why survivorship was also higher during spring on those reefs without adult kelp.

In summary, it seems likely that survival of the transplanted macroscopic juvenile sporophytes was driven by sub-optimal light conditions, and potentially amplified by other abiotic factors. Therefore, whilst the specific causal mechanisms remain to be tested, degradation of adult *E. radiata* habitats appears likely to negatively affect the survival of macroscopic juvenile conspecifics. These findings have clear implications for kelp forest demography and resilience and contribute to our understanding of disturbance-recovery dynamics and kelp forest restoration.

Growth of transplanted macroscopic juveniles

While growth rates of the transplanted juvenile sporophytes increased in general with patch size (Table 4.3), patch size effects were mostly present in the half and natural density treatments. Of these, juveniles transplanted in patches of half kelp density appeared to receive the greatest benefits from increases to patch size (Figs. 4.10, 4.11). Relative to natural kelp density, patches supporting half the natural density of kelp had elevated levels of irradiance, water flow and sedimentation – all of which, above a certain threshold, are potential stressors to developing sporophytes (Wood 1987; Eckman et al. 1989; Wernberg et al. 2005). Accordingly, juvenile kelp in sparser kelp environments might benefit most from increased patch size because the increased abiotic engineering from adult conspecifics helps to ameliorate those potential stressors (Bennett & Wernberg 2014; Bennett et al. 2015).

There was also a trend of higher growth rates in patches of half kelp density, although no significant differences were detected (Figs. 4.10, 4.11). So, while sparser patches of adult kelp can negatively influence survival of juvenile sporophytes (Fig. 4.8), the increased light (Fig. 4.4) may stimulate growth of the remaining sporophytes. Previous work has shown that adult kelp at low density can enhance the growth and development of juvenile kelp relative to dense kelp canopies (Kirkman 1981; Wood 1987; Flukes et al. 2014).

Increases in patch size provided little benefit to the growth of juveniles from the double or zero kelp density treatments (Figs 4.10, 4.11). For the former, any benefits derived from increases in adult patch size may be outweighed by the simultaneous reductions to sub-canopy irradiance and photosynthesis. While for the latter, the lack of a positive patch size effect is not unexpected and is consistent with the suggestion that facilitation by adult kelp contributed to the observed increase in growth rates with patch size.

Irradiance seems a primary influence on both the growth and survivorship of macroscopic juvenile *E. radiata*, and while some increase in irradiance can be deleterious to a portion of the juvenile cohort (see also Toohey & Kendrick 2007), we present evidence suggesting that survivors may experience improved growth under these same conditions. Although, this too will clearly be limited by some upper threshold of irradiance (Wood 1987).

Increased growth of juvenile *E. radiata* after reductions in adult density may enable swift replenishment of the kelp canopy and its engineering capacity. However, this resilience mechanism depends on either the prompt recruitment of *E. radiata* propagules into areas of sparse kelp (which seems unlikely, as discussed below), or the presence of a ‘seed bank’ of juvenile sporophytes already primed within the sub-canopy (Kinlan et al. 2003; Schiel & Foster 2006; Chapter 3).

Recruitment of microscopic sporophytes

No natural recruitment occurred on any of the reefs without adult kelp (Fig. 4.12a), supporting our assumption that reefs were reproductively isolated, and that recruitment could be attributable to only the adult kelp on any given reef. Patch size, but not kelp density, significantly influenced recruitment on the reefs. However, recruitment did occur mostly on patches of double kelp density, and the largest patch from that treatment accounted for more than half of all recruited microscopic sporophytes (Fig. 4.12a). The double density of adult kelp, while not significant, likely influenced supply-side dynamics by producing a greater concentration of zoospores and increased settlement and recruitment success (Reed 1990; Bennett & Wernberg 2014; Tatsumi & Wright 2016). However, given the significant effect of patch size, it seems that ecosystem engineering and the suitability of the physical environment was equally important for the settlement, recruitment and development of microscopic sporophytes on our reefs. This precedence of sub-canopy conditions over spore-supply in shaping *E. radiata* recruitment has been observed elsewhere (see Valentine & Johnson 2005).

Sedimentation in particular has strong negative effects on the microscopic life stages of kelp and other macroalgae, and even small amounts (<50 mg/cm^2) are capable of preventing zoospore attachment (Devinny & Volse 1978) and reducing the survival and growth of kelp gametophytes (Watanabe et al. 2016). Reduced particle size (<599 μm, Watanabe et al. 2016) and increased water flow (Devinny & Volse 1978) exacerbate these negative effects, potentially due to greater particle instability and physical damage from abrasion. We certainly observed that the lowest levels of natural recruitment occurred on reefs with the most accumulated sediments and highest sub-canopy flows. Related to sedimentation is the formation of turf algae that trap sediment particles to form a turf-sediment matrix, which inhibit the recruitment of juvenile *E. radiata* (Kennelly 1987b). However, whether this inhibition is due to the turf itself, the trapped sediment particles, or some other factor is still unclear and warrants further investigation.

As discussed, light and kelp scour influence the formation of turf algae, but these factors might have additional impacts on the settlement and recruitment of kelp. Despite somewhat variable results depending on the species and developmental stage in question, deleterious effects of increased irradiance on microscopic life stages of kelp have been reported (Altamirano et al. 2004; Cie & Edwards 2008). Kelp scour meanwhile may negatively affect kelp propagules via abrasion, as suggested by Dayton et al. (1984), but may also promote settlement and recruitment by deterring herbivory (Velimirov & Grifitths 1979; Toohey et al. 2004). Previous work has also demonstrated that the amount of scouring in small patches of *E. radiata* can be minimal (Chapter 2). Overall, we observed that microscopic sporophytes occurred mostly on microscope slides that had minimal cover

of turf and sediment and hence is it seems that scour from the adult kelp was likely a positive force for recruitment on our reefs.

In addition to indirect and synergistic effects, elevated water flow may directly influence the settlement and recruitment of *E. radiata* propagules. Lower water velocities have been observed to aid the settlement and survival of the propagules of kelp and other large brown habitat-forming macroalgae (e.g. Order Fucales) (Devinny & Volse 1978; Serrão et al. 1996). Moreover, hydrodynamics beneath intact kelp canopies are characterised by low turbulent mixing and high particle retention relative to areas external the canopy (Eckman et al. 1989). Such conditions may facilitate retention, settlement and recruitment of propagules within the sub-canopy (Dayton et al. 1992; Graham 2003; Smale et al. 2011). This notion is supported by our findings of decreasing sediment deposition in smaller patches, because the same fine-scale hydrodynamics that influence the settling of sediment particles likely extend to other small particles such as kelp propagules (Eckman et al. 1989; Serrão et al. 1996).

We conclude that the recruitment of *E. radiata* microscopic sporophytes will be negatively affected by reductions to patch size. This is likely influenced by increased levels of sedimentation, and potentially water flow, irradiance, and the breakdown of hydrodynamic processes that facilitate the retention and settlement of propagules within the sub-canopy. The provision of suitable habitat and the amelioration of physical stress via engineering by adult *E. radiata* appears central to facilitating recruitment of juvenile conspecifics.

Survival of microscopic sporophytes

Most of the microscope slides became heavily fouled with turf algae-sediment matrices over the outplanting period. By outplanting already established microscopic sporophytes, we attempted to isolate any problems of sediments interfering with propagule attachment. Despite this, survivorship of the microscopic sporophytes was still very low in most circumstances. While high mortality was not unexpected given the 'low cost-high volume' reproductive strategy of kelp (Chapman 1984; Schiel & Foster 2006), the results suggest that impediments to propagule attachment are not the only factors shaping survival of microscopic life stages.

Increasing patch size significantly improved survivorship of the outplanted microscopic sporophytes, and there was a strong, but non-significant, trend for survivorship to increase with kelp density (Fig. 4.12b, Table 4.3). No surviving sporophytes were observed on any reefs smaller than 1 m^2 or without adult kelp, further illustrating the importance of adult *E. radiata* to the development of juvenile conspecifics. Some experimental patches that experienced no natural recruitment did still have surviving outplanted microscopic sporophytes (Fig. 4.12). This indicates that some patches that were suitable for the survival of microscopic sporophytes were not suitable for recruitment or failed to receive an adequate supply of propagules.

Our observations reveal that the microscopic life stages of *E. radiata* are not only impaired in areas without adult conspecifics, but also in areas without a sufficient density or patch size of adults. This suggests that the recruitment and survival of microscopic juveniles in areas where adult conspecifics are sparsely or patchily distributed can be much lower than on reefs with intact and continuous cover of *E. radiata.*

Recruitment of macroscopic juveniles

The natural recruitment of macroscopic juveniles occurred on fewer than half of the patch reefs, with no recruits observed on any of the reefs without adult kelp, further reinforcing our assumption of reproductive isolation between reefs. The density of recruits we observed on many of the experimental reefs was similar to densities of stage 1 juveniles recorded in natural *E. radiata* habitats (Kirkman 1981; Toohey & Kendrick 2007; Chapter 3).

We detected clear effects of patch size and kelp density, with recruits occurring at higher densities in larger patches and, during the winter census, also in patches reefs supporting higher densities of adult kelp. The trend for increasing recruitment with adult kelp density was also evident during the censuses in spring and at the end of the study. The greater number and density of recruits evident at the end of the study (Fig. 4.13) may reflect annual variations in peak recruitment (which occurs during winter and spring, Chapter 3) or succession and stabilisation of the sub-canopy community over time (Dayton et al. 1992; Toohey et al. 2007; Smale et al. 2011). Recruitment on patches <2 m^2 was infrequent, indicating that there may be a threshold patch size for natural recruitment, although the threshold seems to be lower at higher densities of adult kelp (Fig. 4.13). A threshold minimum patch size for effective recruitment of *E. radiata* recruitment may arise through density-dependent processes (Reed 1990), and/or reflect ecosystem engineering and the local environmental conditions (Bennett et al. 2015).

The pattern of recruitment of macroscopic sporophytes was similar to that of recruitment and survivorship of the microscopic sporophytes, particularly on reefs supporting adult kelps at double natural density, which showed the highest measures of these demographic processes. The sub-canopy environment on those patches, particularly when larger than ~2 m^2, must represent optimal conditions for the recruitment of microscopic and macroscopic juvenile *E. radiata.* Interestingly however, our results reveal that these conditions are not ideal for the growth of juvenile sporophytes (Fig. 4.10). In these circumstances, once the juvenile *E. radiata* reaches a certain size growth must slow or cease to await improved conditions (Kirkman 1981; Toohey & Kendrick 2007). Ultimately, recruitment was absent in areas lacking sufficient adult kelp, and we expect that recruitment of *E. radiata* into degraded habitats could be significantly compromised by changes to the abiotic and biotic environments.

Environment-engineer feedback

Ecosystem engineering by adult *E. radiata* seems to create conditions that facilitate juvenile conspecifics. However, the capacity of this species to modify the environment to the benefit of the next generation is weakened by reductions in patch size and kelp density. Thus, habitat degradation leads to changes in local abiotic and biotic conditions within the sub-canopy, which feedback to impair demographic rates. Subsequently the reestablishment of an intact kelp canopy is hindered, potentially leading to an increasingly altered sub-canopy environment and a downward spiral of demographic rates. This process represents the loss of a positive environment-engineer feedback and explains the pattern of impaired recruitment and development of juvenile kelp that we observed to occur with habitat degradation.

Previous studies have highlighted the poor re-establishment of *E. radiata* that occurs after large areas (39–314 m^2) have been cleared of adult canopy (Kirkman 1981; Toohey et al. 2007). More surprising, is that the first signs of recovery can take longer than 9 months to occur (Kirkman 1981), and that full canopy recovery can take in excess of 3 years (Toohey et al. 2007). However, each of these studies describes the rapid and opportunistic establishment of other macroalga into the cleared areas, including species of *Ulva, Enteromorpha,* and *Sargassum.* Further, Valentine & Johnson (2005) demonstrated that even after heavy inoculation of *E. radiata* spores, no recruitment occurred into an area that had been cleared of a macroalgae canopy. Widespread loss of adult *E. radiata* may therefore result in long-term localised absences of kelp, which may require interspecific facilitation, successional processes, or habitat restoration for reestablishment.

Evidence of intraspecific facilitation by adult *E. radiata* is also indicated in that when cleared areas do slowly recover, they are recolonised by juveniles from the outside inwards (Kennelly 1987a; Kennelly & Underwood 1993). This indicates that new growth, and thus settlement, post-settlement survival, and/or recruitment of juvenile *E. radiata* is occurring preferentially and more successfully in close proximity to adult conspecifics. Likewise, when small areas of *E. radiata* are cleared, the recruitment and growth of juveniles and replenishment of the canopy is rapid (Kirkman 1981; Flukes et al. 2014). As demonstrated by our results however, this process appears dependent on existing juveniles within the sub-canopy at the time of disturbance, rather than the opportune recruitment of sporophytes into disturbed areas (see also Toohey & Kendrick 2007; Chapter 3).

The pattern of demographics in *E. radiata* seem to differ from those observed in several other kelp (see Dayton et al. 1984, 1992; Reed 1990; Schiel & Foster 2015). These studies described that the juveniles of several species – including *Macrocystis pyrifera, Laminaria farlowi* and *Pterygophora californica* – do not typically survive or grow beneath the adult canopy, even when transplanted/inoculated. Instead, they seem to thrive preferentially in areas with no (or very sparse) kelp canopy, primarily due to competition for light. Furthermore, experimentally cleared patches of

these species are typically re-colonised from the inside outwards (Dayton et al. 1992; Schiel & Foster 2015).

Patch size effects consistently appeared to be of greater significance than kelp density effects in determining the engineering capacity of *E. radiata* (Table 4.3). In fact, our results suggest that the demographic processes of juvenile *E. radiata* may actually benefit from variations in adult kelp density. In general, patches supporting adult kelp at the average natural density provided an ideal environment for juvenile *E. radiata*. Yet, patches of sparser kelp appeared to favour the growth of already established macroscopic juveniles (Figs. 4.10, 4.11), while patches of denser kelp seemed the best environment for the recruitment and survival of the microscopic sporophytes (Fig. 4.12). This has interesting implications for our understanding of habitat mosaics and successional dynamics within intact canopies of *E. radiata*, but also for the restoration of degraded kelp habitats.

Ultimately, we suggest that the survival of the early life stages of *E. radiata* may be as much to do with the amelioration of physical stressors as access to abiotic resources. Such that intraspecific facilitation by adult *E. radiata* expands the 'realised niche' of juvenile conspecifics, through the amelioration of potential stressors such as high sedimentation and deleteriously high light levels (see Dayton et al. 1999; Bulleri 2009; Crotty & Bertness 2015). The amelioration of physical stressors and the Stress Gradient Hypothesis have been previously applied to explain facilitation in classically stressful environments, such as the intertidal (Crain & Bertness 2006; Bulleri 2009). Despite the somewhat more benign conditions on subtidal reefs, even a subtle improvement of sub-canopy conditions for juvenile *E. radiata* by adult conspecifics could have large implications when applied across the scale of populations (Dayton et al. 1999; Crain & Bertness 2006; Bennett & Wernberg 2014; Bennett et al. 2015).

Conclusion

We demonstrate the ability of the kelp *E. radiata* to modify the physical environment and influence levels of water flow, irradiance and sedimentation in the sub-canopy environment. However, this engineering ability is dependent on patch size and, to a lesser extent, the density of adult kelp. Our results suggest that degradation of *E. radiata* stands, realised as reductions in patch size and adult kelp density, are likely to dramatically alter local abiotic and biotic conditions, with strong feedbacks that negatively affect the species' microscopic and macroscopic juvenile life stages. The specific mechanisms responsible for the inhibition – and sometimes collapse – of the demographic processes of juvenile *E. radiata* remains to be investigated. However, we illustrate the potential for complex, cumulative and synergistic interactions between potential stressors. While it seems the microscopic stages of *E. radiata* are likely to be most affected by the loss of adult conspecifics, macroscopic juveniles may possess some capacity (via increased growth rates) to aid the rapid recovery of the canopy following a disturbance. However, because this mechanism relies on a

'seed bank' of juveniles within the sub-canopy at the time of disturbance, disruption to the microscopic life stages seems likely to impair replenishment of the seed bank and long-term habitat stability.

Our results are consistent with the hypothesis that ecosystem engineering by adult *E. radiata* facilitates the development of the juvenile conspecifics. Habitat degradation can impair the ability of *E. radiata* to engineer change, causing a breakdown in the positive environment-engineer feedback, leading to the collapse of demographic functions and reduced ecosystem stability and resilience.

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Appendices

Appendix 4.1 Results of ANCOVAs illustrating no effects of kelp density, patch size, time of day or season on above canopy (i.e. ambient) abiotic factors. Output is for unsaturated models after confirming homogeneity of slopes. Response variable (Y) and associated transformation is noted in the first column.

data analysed	*factor*	*SS (df)*	*F*	*P*
WATER FLOW				
winter $(Y)^{2.00}$	kelp density	86907 (1,25)	1.240	0.276
	patch size	190274 (1,25)	2.715	0.112
spring $(Y)^{1.80}$	kelp density	911 (1,25)	0.149	0.703
	patch size	22882 (1,25)	3.739	0.065
SEDIMENT DEPOSITION				
autumn $(Y)^{-0.13}$	kelp density	0.001 (1,24)	0.536	0.471
	patch size	0.001 (1,24)	1.140	0.296
winter	kelp density	933 (1,22)	0.257	0.618
	patch size	13042 (1,22)	3.587	0.071
spring $(Y)^{0.45}$	kelp density	4.400 (1,24)	2.675	0.071
	patch size	0.001 (1,24)	0.005	0.945
summer $\log(Y)$	kelp density	0.031 (1,25)	0.244	0.625
	patch size	0.001 (1,25)	0.001	0.924
IRRADIANCE				
spring $(Y)^{-0.65}$	kelp density	1.51^{e-5} (1,109)	0.730	0.395
	patch size	7.24^{e-5} (1,109)	3.503	0.064
spring $(Y)^{-0.65}$	time of day	$4.40e^{-6}$ (1,109)	0.212	0.672
	patch size	$4.65e^{-5}$ (1,109)	3.683	0.058

Chapter 5. Chemical microenvironments within macroalgal assemblages: implications for the inhibition of kelp recruitment by turf algae

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Abstract

Kelp forests around the world are under increasing pressure from anthropogenic stressors such as pollution and climate change. A widespread consequence of this degradation is that in many places, complex and highly productive kelp habitats 'phase shift' to become dominated by structurally simple and less productive turf algae. These turf algae habitats resist re-establishment of kelp via recruitment inhibition, however relatively little is known about the precise mechanism(s). One possible influencing factor is the chemical environment within the turf-sediment matrices into which kelp propagules settle and develop. In laboratory trials, we compared the chemical microenvironments (i.e. O_2 concentration and pH, 0.1–50 mm above the benthos) within four multispecies macroalgal assemblage (including a natural turf-sediment assemblage and a kelp-dominated assemblage) to examine whether differences in the chemical microenvironments may contribute to the inhibition of kelp recruitment by turf algae. Our results illustrate that the chemical environments within each macroalgal assemblage were characterised by elevated O_2 concentrations and pH relative to the surrounding seawater. Critically however, these conditions were significantly higher within the turf-sediment assemblage than in the kelp-dominated assemblages. These conditions can cause reductions in the photosynthetic or physiological potential of kelp propagules, and thus may impair their ability to survive and develop within turf algae assemblages. Indeed, field observations of the assemblages prior to lab trials reflected that recruitment of kelp was significantly greater in the kelp-dominated assemblage than in treatments with dense turf algae. More work on the ecophysiology of kelp (particularly the microscopic stages) is needed before identifying the precise mechanisms of recruitment inhibition, however, these results increase understanding of how the degradation of kelp habitats can result in the proliferation and persistence of turf algae habitats and, localised absences of kelp.

Introduction

Kelp (Order Laminariales) and other large brown canopy-forming macroalgae (e.g. Order Fucales) dominate coastal environments in temperate and subpolar latitudes around the world (Steneck et al. 2002; Krumhansl et al. 2016). These macroalgae create spatially complex habitats and altered sub-canopy environments that support diverse and productive ecosystems (Graham et al. 2007; Bennett et al. 2016; Teagle et al. 2017). However, in many places, kelp forests are being degraded by rising ocean temperatures (Johnson et al. 2011; Krumhansl et al. 2016; Wernberg et al. 2016), overgrazing (Ling et al. 2015; Vergés et al. 2016), and eutrophication (Graham et al. 2007; Gorman & Connell 2009; Airoldi & Beck 2011). A widespread consequence of this degradation is that complex and highly productive kelp habitats phase shift and become dominated by structurally simple and less productive 'turf algae' (Steneck & Johnson 2014; Strain et al. 2014; Filbee-Dexter & Wernberg 2018).

Turf algae define a multitude of short turf-forming species of alga (reviewed by Connell et al. 2014). Those that typically replace kelp habitats are a multispecies assemblage of short branching or filamentous green and/or red alga, which form dense turfs and trap sediments to create a turf-sediment matrix where few other large macroalgae persist (Kennelly 1987; Connell et al. 2014; Strain et al. 2014).

On temperate reefs around the world, kelp and turf algae habitats exist as alternative stable states, with each state inhibiting the formation of the other (Steneck & Johnson 2014; Strain et al. 2014; Filbee-Dexter & Wernberg 2018). Shading and physical abrasion by the kelp are the primary mechanisms that inhibit the proliferation of turf algae beneath kelp canopies (Kennelly 1987; Dayton et al. 1984; Irving & Connell 2006). Thus, external disturbances of the canopy – which may be natural (e.g. storms, Dayton & Tegner 1984) or anthropogenic (e.g. eutrophication, Gorman & Connell 2009) – are required to instigate phase shifts from kelp to turf-dominated states (Kennelly 1987; Steneck & Johnson 2014). Moreover, once a phase shift has occurred, and even after the initial disturbance has passed, hysteresis in the system can ensure that turf algae persist and prevent the re-establishment of kelp (Gorman & Connell 2009; Steneck & Johnson 2014; Filbee-Dexter & Wernberg 2018). It stands that understanding phase shifts and the persistence of turf algae is a key objective in the management and conservation of kelp forests around the world (Steneck & Johnson 2014; Johnson et al. 2017; Filbee-Dexter & Wernberg 2018).

Turf algae prevent kelp re-establishment through the inhibition of kelp recruitment (Dayton et al. 1984; Kennelly 1987; Strain et al. 2014). Despite this widespread phenomenon, relatively little is known about the specific mechanisms that cause recruitment inhibition of kelp by turf algae. The ubiquitous sediments within turf assemblages likely inhibit the settlement and recruitment of kelp propagules via smothering, abrasion and substratum instability; however, this has only been

investigated for a handful of kelp species (Devinny & Volse 1978; Geange et al. 2014; Watanabe et al. 2016). One factor that has been largely overlooked as a potential mechanism is the chemical environment within turf algae assemblages (discussed by Dayton et al. 1984; Kennelly 1987; Schiel & Foster 2006). The scant existing research suggests the environment within filamentous algae assemblages may be prone to oscillations between anoxia and hyperoxia (Pöhn et al. 2001; Hauri et al. 2010), and may therefore create poor chemical environments for the settlement and development of the microscopic kelp propagules (Kennelly 1987; Schiel & Foster 2006; Hurd et al. 2014).

Seawater chemistry within macroalgal habitats is altered predominately by the metabolic processes of the algae, which can cause diel fluctuations of pH, oxygen (O_2) and dissolved inorganic carbon (DIC) (Hurd et al. 2011, 2014; Britton et al. 2016). During the day, uptake of carbon dioxide (CO_2) and release of O_2 by algae during photosynthesis decreases DIC availability and increases pH and O_2 concentration. At night, respiration releases CO_2 and the absence of photosynthesis causes net-consumption of O_2, resulting in reductions in pH and O_2 concentration and increasing DIC concentration (Middelboe & Hansen 2007; Hurd et al. 2011). These processes are typically regulated by concentration boundary layers (CBL) that form at the surface of the macroalgae and substratum at scales of micro- to millimetres (Hurd et al. 2011; Cornwall et al. 2013). Ensuring that the chemical microenvironment immediately surrounding macroalgae and the benthos can differ greatly from the mainstream seawater (Hurd et al. 2011, 2014). It is in this benthic microenvironment where the settlement and recruitment of kelp and the associated community occurs (Reed 1990; Schiel & Foster 2006; Teagle et al. 2017).

Ecklonia radiata is the most widespread habitat-forming kelp in Australasia. This stipitate kelp (*sensu* Dayton et al. 1984) rarely grows taller than 1.5 m, but creates complex and highly productive habitats (Wernberg et al. 2005; Bennett et al. 2016). Like all kelp, mature *E. radiata* sporophytes release zoospores that settle and germinate into male or female gametophytes (Reed 1990; Schiel & Foster 2006). Once fertilised by the motile male sperm, the sessile female gametophyte acts as the base from which the sporophyte develops. *Ecklonia radiata* habitats in Australia, like many other kelp habitats around the world, are under increasing pressure from anthropogenic stressors (Gorman & Connell 2009; Bennett et al. 2016; Wernberg et al. 2016). Already, highly productive and biodiverse *E. radiata* habitats have undergone phase shifts to less productive and less biodiverse turf habitats (Valentine & Johnson 2005; Gorman & Connell 2009; Filbee-Dexter & Wernberg 2018). Moreover, these shifts are expected to continue and potentially even increase in the future (Connell et al. 2013; Falkenberg et al. 2015).

The aims of this study were, to characterise and compare the chemical microenvironments within four multispecies macroalgal assemblages and, to explore whether differences in the chemical microenvironments may contribute to the inhibition of kelp recruitment by turf algae. To this end, we

compared vertical profiles (0.1–50 mm above the benthos) of O_2 concentration, pH and CBL thickness within a (i) natural turf-sediment assemblage to: (ii) a natural kelp assemblage dominated by *Ecklonia radiata*; (iii) an assemblage of understorey algae (i.e. without canopy-forming species), and; (iv) a turf assemblage with the entrained sediments removed. This final comparison allowed examination of the effects of the turf algae in isolation from the ubiquitous entrained sediments. Profiles of the microenvironments were measured in a flume tank at levels of light (~100 μmol photon m^{-2} sec^{-1}) and water velocity (~6 cm/sec) representative of field conditions to allow maximum applicability of the results. Additionally, recruitment of juvenile kelp to the macroalgal assemblages (except the treatment of turf with the entrained sediments removed, which could only be established in the lab) was quantified in the field to determine the recruitment potential of each assemblage. Our goal was to better understand the mechanisms of how turf algae assemblages inhibit kelp recruitment.

Methods

Macroalgal assemblages and *in situ* assessments of kelp recruitment

In June 2015 (austral winter), sandstone pavers (150 x 150 x 20 mm) were installed at Fortescue Bay, Tasmania, Australia (-43.13735, 147.96819) to develop distinct macroalgal assemblages. The site is semi-exposed and subject to occasional ocean swell, with reef that is dominated by *Ecklonia radiata* (Flukes et al. 2014 provide a detailed description of the macroalgal community at the site). Twenty pavers were attached to a mesh rack secured to the benthos at a depth of 14 m within a small gap in the *E. radiata* canopy. Five replicate pavers were allocated randomly to one of four experimental treatments and remained in the field for 260 days until February 2016 (austral summer).

Three distinct macroalgal assemblage types were cultivated in the field; (1) an *E. radiata*-dominated assemblage; (2) an assemblage of only understorey alga; and (3) a turf algae assemblage, of which half were later modified in the lab by removing the entrained sediment to create the fourth experimental treatment (Fig. 5.1). The *E. radiata*-dominated assemblage was cultivated by allowing undisturbed colonisation of the pavers. These pavers simulated an intact kelp habitat and contained a small canopy of *E. radiata* (≤ 250 mm in height) with a diversity of smaller understorey and coralline algae. The treatment consisting only of understorey algae was cultivated by removing any canopy-forming species from those pavers (largely *E. radiata,* but also *Cystophora* sp.). Assemblages similar to this typically occur within small canopy-gaps and are part of the natural dynamics of *E. radiata* habitats (Irving & Connell 2006; Flukes et al. 2014). The turf algae assemblage was cultivated by removing both canopy-forming species and large understorey algae (typically *Ulva* sp.) to decrease shading and promote the establishment of the turf-sediment matrix. Small ephemeral patches of turf-sediment matrix also occur naturally within kelp habitats, typically in areas free of canopy-forming macroalgae (Irving & Connell 2006). Half of the pavers supporting turf algae assemblages were

modified in the lab immediately prior to profiling by gently flushing the sediments from the turf algal matrix using filtered seawater. There were n = 5 replicates of each of the four experimental assemblages, plus n = 5 replicates of a control treatment consisting of bare pavers that had been stored in filtered and aerated seawater for 260 days. Hereafter, the treatments are referred to as Control; Kelp; Understorey; TSM – the unmodified turf-sediment matrix; and Turf – the turf algae assemblage with sediments removed (abbreviated as Con, Kelp, US, TSM and Turf, respectively).

To assess the effects of the macroalgal assemblages on kelp recruitment, all visible *E. radiata* recruits (>5 mm) were quantified on these treatments at 50, 148, and 260 days after installation. Except for the Kelp treatment, recruits were removed from pavers at the time of counting and analyses were conducted using cumulative recruitment on those treatments.

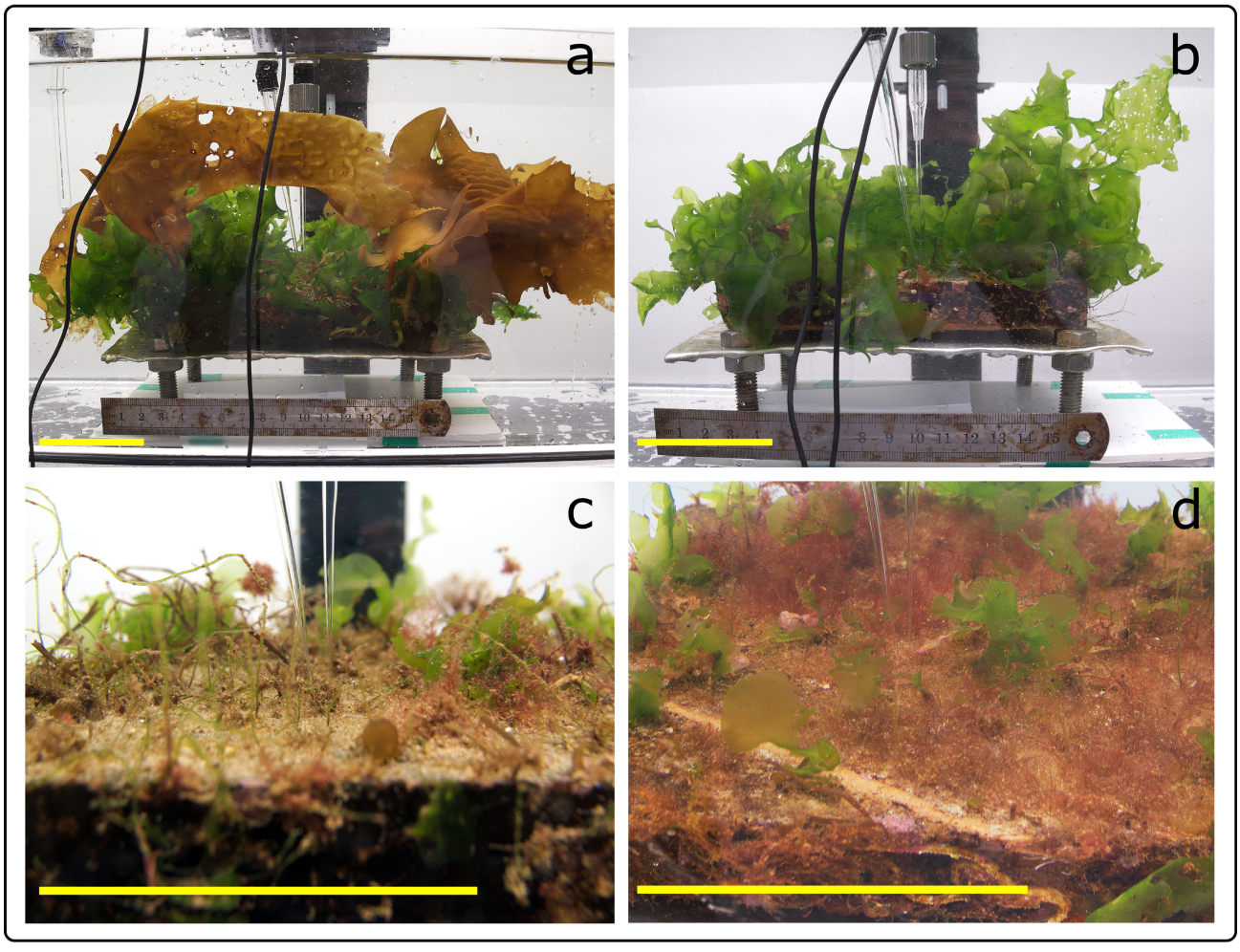

Figure 5.1 Representatives of the four experimental macroalgae assemblages: (a) Kelp, an algal assemblage dominated by the kelp *Ecklonia radiata*; (b) US, an assemblage of understorey algal species; (c) TSM, a turf algae-sediment matrix assemblage, and; (d) Turf, a turf algae assemblage with entrained sediments largely removed. The yellow scale bar in each image represents ~50 mm.

Lab-conditions and experimental protocol

Immediately prior to collection of the experimental assemblages in February 2016, the depth of the sediments within any turf-sediment matrix was measured to the nearest 1 mm at two standardised locations on each paver (50 mm from the edges). This provided an estimate of sediment accumulation for each treatment. The pavers and their attached assemblages were then removed from the rack and placed in individual containers for transport to the laboratory.

In the lab, pavers were placed in individual 13 L plastic buckets filled with filtered and aerated seawater under 30 ± 2 μmol photon m^{-2} sec^{-1} (± SE, n = 12) and a 12:12 light cycle, all within a temperature-controlled room at 15°C. Each day, 5 L of the seawater in the storage buckets was replaced. Light was provided by hydroponic fluorescent tubes and measured using a LI-COR LI-192 2π quantum sensor. All seawater used throughout the experiment was from a 10,000L tank of oceanic seawater that was UV sterilised and filtered (0.2 μm pore-size).

Trials of the experimental assemblages within the flume were done in random order and completed over 7 days. The macroalgal assemblages displayed no signs of stress or deterioration (e.g. pigment loss, necrosis) over the length of the experiment and we detected no effect of 'day of trial' on the results.

Experimental flume

Trials were conducted within the flume tank described by Cornwall et al. (2013) but was filled with a greater volume of seawater (55 L) than in previous uses (46 L). This is a recirculating unidirectional laminar flow flume with an 850 x 200 mm (L x W) testing section. The flume was filled with filtered seawater to a depth of 200 mm and operated within a temperature-controlled room at 15 °C. Mean seawater temperature within the flume recorded before each trial was 15.2 ± 0.1 °C (± SE, n = 25). After every second trial, the flume was vigorously rinsed, and the full volume of seawater replaced. Trials were conducted under an irradiance of 103 ± 5 μmol photon m^{-2} sec^{-1} (± SE, measured at the start and end of each day, n = 14) provided by hydroponic fluorescent tubes. This is a typical level of irradiance experienced by *E. radiata* and associated macroalgal communities in the field (Wernberg et al. 2005; Flukes et al. 2014; Chapters 2 & 4.). Water velocity in the middle of the water column in the flume was measured using a SonTek MicroADV (Acoustic Doppler Velocimeter) at 10 MHz on the horizontal axis in the direction of flow. Trials were conducted at a water velocity of 6.08 ± 0.03 cm/sec (± SE, n = 600). This velocity simulates field conditions (Kregting et al. 2011, unpubl.) and is within the upper range used during previous microprobe studies (Cornwall et al. 2014, 2015). It was not possible to accurately measure water velocity within the macroalgal assemblages due to interference of the sensor by algae. We instead measured water velocity downstream of one random replicate from the control and each of the unmodified macroalgal assemblages (i.e. Kelp, Understorey & TSM). This enabled a relative comparison of their capacity to reduce flow.

Profiling the chemical microenvironment of macroalgal assemblages

Vertical profiles of O_2 concentration (μmol/L) within the assemblages were measured using a Unisense OX-50 O_2 microprobe with a 50 μm tip mounted to a MM33-2 MicroProfiling system (vertical accuracy ± 10 μm) and connected to a OXY-Meter signal-amplifier. The profiles were recorded using Unisense Logger software (v. 2.7), and the O_2 microprobe calibrated as per manufacturer's instructions using solutions of 0 and 100% O_2 saturation.

For each trial, a randomly selected paver was placed in the testing section of the flume on a stand 40 mm above the base of the tank. The stand ensured consistent positioning beneath the micromanipulator and minimal disruption of laminar flow. After placing the assemblage within the flume, the trial commenced and an initial 1-minute measurement of O_2 concentration in the mainstream water was recorded ~50 mm upstream of the paver. The microprobe was then lowered to the surface of the benthos in the approximate centre of the paver (this position was designated as '0.0 mm'). The microprobe remained at 0.0 mm for 60 minutes to allow O_2 concentrations to stabilise (determined from preliminary measurements). Vertical profiling then commenced with 1-minute measurements at 0.0 mm, then at 0.1 mm increments between 0–1 mm, and then at 2, 4, 8, 16, 32 and 50 mm above the benthos (50 mm was the greatest distance the micromanipulator could be accurately withdrawn from the benthos). This range provided high-resolution sampling of the benthic microenvironment in which kelp propagules settle (0–1 mm), followed by a progression through the remaining turf and understorey algae. Following the last profile measurement at 50 mm, a final 1-minute mainstream measurement was recorded in the same position as the initial mainstream measurement. O_2 concentration at every position – including mainstream measurements – was calculated as the mean of 60 measurements recorded over the 1-minute sample.

It was not possible to accurately and robustly measure the biomass of the macroalgae in the immediate vicinity of the microprobe. However, the biomass (dry weight g) of each replicate was quantified by removing all macroalgae from the paver immediately following each trial. Macroalgae were then identified to species level (or genus/functional group where this was not possible) and then dried at 60 °C until constant mass (~24 hours). See Appendix 5.1 for taxa and biomass data.

Data analysis and statistics

Data from one replicate of the TSM treatment was excluded from all analyses due to microprobe malfunction. Subsequent analyses were left unbalanced except in one instance where a balanced-design was required (details below). Following Cornwall et al. (2014), values of pH were derived from a linear relationship ($r^2 = 0.97$, from Noisette & Hurd in press) between O_2 saturation and total pH (pH_T; all subsequent measurements are referred to on the total scale). Our measures of O_2 concentration were transformed to O_2 saturation using the Unisense tables of O_2 solubility.

CBL thickness was estimated from the mean profiles of each treatment and, defined as the greatest height above the benthos at which O_2 concentration was >5% different from mainstream values. This approach balances the robustness (>10% difference, Hurd et al. 2011; Cornwall et al. 2013) and sensitivity (>1% difference, Cornwall et al. 2015) of previous methods to estimate CBL thickness surrounding macroalgae in flumes.

Data were primarily analysed using analysis of variance (single factor ANOVA) with 'Treatment' as a fixed factor, followed by multiple comparisons using *a priori* contrast sets when the overall ANOVA indicated significance. Test assumptions were assessed using diagnostic plots of model residuals (to check normality, linearity and homoscedascity), and data that did not meet test assumptions were transformed based on values of λ from Box-Cox plots, which is noted in the model output. The addition of a small constant was required to ensure an appropriate transformation when the response variable was zero and, is noted in the model output. *A priori* contrasts were limited to directly address the experimental aims, *viz.* TSM vs Kelp, TSM vs Understorey, TSM vs Turf, and Control vs macroalgal assemblages. This latter contrast was not used when the Control had no response variable (i.e. macroalgal biomass, recruitment). The set of *a priori* contrasts were not orthogonal, so *P*-values were adjusted using the single-step method (Bretz et al. 2011). For the analysis of flow-reduction by the macroalgal assemblages no *a priori* contrasts were defined, and so unplanned multiple comparisons were conducted using Tukey's Honest Significant Difference test. A two-tailed *t*-test was also used to test whether Control trials changed mainstream bulk water. Note that for analysis of the field data (i.e. kelp recruitment, sediment accumulation), the TSM and Turf treatments are functionally identical, since the Turf treatment was only established in the lab after collection.

Linear (Kelp and Understorey) and nonlinear (TSM and Turf) regression was used to derive models of the profiles for each treatment. The dependent variable 'height above benthos' was log transformed to meet test assumptions, and models were fitted to data from the vertical profiles only (i.e. mainstream values were excluded). Linear models were fitted using simple regression, and a second-order polynomial term used when fitting the Kelp treatment model. Nonlinear models were fitted using an iterative process based on a negative asymptotic exponential function and re-fitted using different starting parameters to ensure reliability (Quinn & Keough 2002) (although the best fit for each model was always achieved on the first attempt). Comparison of Kelp vs Understorey, and TSM vs Turf profiles were then made using a Vuong closeness test (Rivers & Vuong 2002), which tests non-nested models against the null hypothesis that the two models do not differ. This required a fully balanced design, and so a random replicate at each profile height from the Turf treatment was omitted to provide balance against the TSM treatment ($n = 4$). Obvious differences between the linear and nonlinear O_2 profiles (e.g. Kelp vs TSM) rendered additional comparisons unnecessary and illogical.

Canonical analysis of principal coordinates (CAP) were used to illustrated multivariate community structure between experimental assemblages. CAP routines were based on Bray-Curtis similarity matrices of fourth-root transformed data and conducted on the full algae dataset and a reduced dataset that excluded *E. radiata* and *Ulva* sp. given that abundances of these two species were experimentally modified.

Analyses were conducted using the *multcomp* (post-hoc multiple comparison testing), *nls* (nonlinear regression), and *nonnest2* (Vuong closeness test) packages in *R* (v. 3.2.5; *R* Core Team), with alpha at $\alpha = 0.05$. *PRIMER 6* (v. 6.1.18) was used for CAP analyses. Figures are presented with untransformed variables for clarity, and were produced using *R, PRIMER 6* and *Inkscape* (v. 0.91).

Results

Kelp recruitment and macroalgal assemblages

At the time of the first assessment 50 days after initial deployment, there were no significant differences in *Ecklonia radiata* recruitment across the experimental assemblages (Fig. 5.2i, Table 5.1). By the time of the second assessment 148 days after installation, the macroalgal assemblages were much more developed and there was significantly more *E. radiata* recruits on the pavers with the Kelp treatment compared to the other treatments, which were all similar (Fig. 5.2ii, Table 5.1). Less kelp recruitment occurred after this, but by 260 days, recruitment of *E. radiata* was still significantly greater on the Kelp pavers compared to the other treatments, which were all similar (Fig. 5.2iii, Table 5.1). At the time of collection, most *E. radiata* that had recruited to the Kelp treatment had developed into small (≤ 250 mm) stage 2 sporophytes (*sensu* Kirkman 1981). No recruits were reproductively mature (based on the morphology and absence of sori, Novaczek 1984), and thus we could discount the possibility of self-recruitment.

Differences in macroalgal community structure among the treatments were clear (Fig. 5.3i). The Kelp treatment was distinct from other treatments due to presence of *E. radiata* and geniculate coralline algae and absence of filamentous turf algae and *Cystophora* sp. The Understorey treatment was mostly differentiated from the turf algae treatments (i.e. TSM & Turf), and these three treatments were classified along an axis of increasing branching and foliose red alga in the Understorey treatment and increasing filamentous algae in the two turf treatments. Two species of brown understorey alga were also important to assemblage differentiation, with *Halopteris paniculata* characteristic of the two turf assemblages and *Carpoglossum confluens* typical of the Kelp and Understorey treatments.

Less overall differentiation among the treatments was apparent in the analysis excluding the canopy-forming kelp *E. radiata*, and the large understorey alga *Ulva* sp. (Fig. 5.3ii), i.e. focussing on the macroalgae that were not directly manipulated. Nonetheless, the understorey community on the Kelp treatment was still relatively separate to that of the other treatments, but unlike the initial CAP,

was more similar to the Understorey treatment. In turn, the Understorey treatment was grouped among the spread of the two turf treatments. Similar taxa as in the initial CAP (with the obvious exceptions of *E. radiata* and *Ulva* sp.) were responsible for driving among-group differences.

Not surprisingly, total macroalgal biomass differed significantly among the treatments and was highest in the Kelp treatment (Fig. 5.4i, Table 5.1). The biomass of turf algae within each assemblage also differed significantly among treatments and was highest in the TSM treatment (Fig. 5.4ii, Table 5.1). The depth of the turf-sediment matrix on the pavers at the time of collection also differed significantly across treatments (Fig 5.4ii), with the two turf algae treatments having the thickest turf-sediments, followed by the Understorey and then Kelp treatments (Table 5.1).

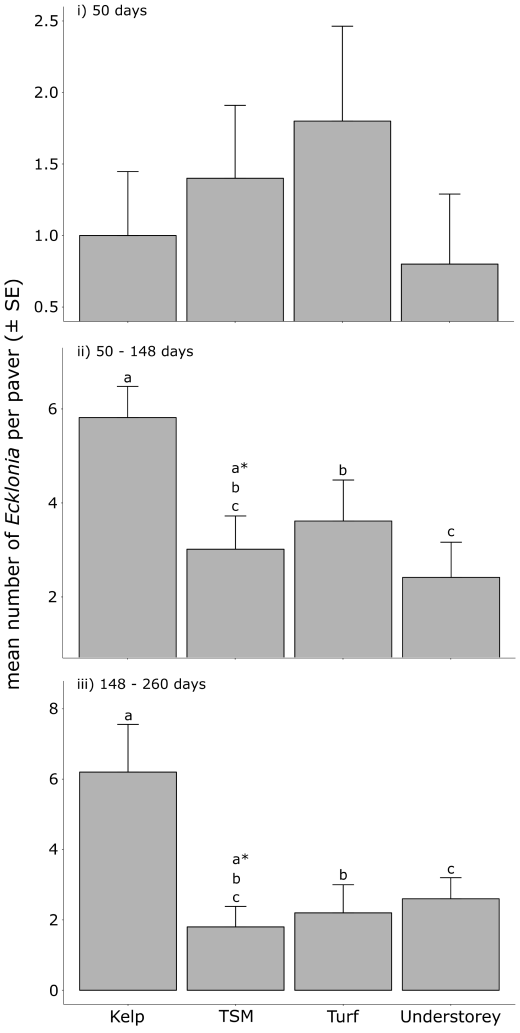

Figure 5.2 Mean kelp (*Ecklonia radiata*) recruitment in the experimental macroalgae assemblages across three sample periods (i-iii). No significant differences were detected during (i) the first sample period. Outcomes of post-hoc *a priori* comparison tests are noted for (ii, iii) the second two periods: similar letters denotes the pairwise comparison and an asterisk indicates significant pairwise differences (Table 5.1). Experimental treatments are Kelp, an algal assemblage dominated by the kelp *Ecklonia radiata;* Understorey, an assemblage of understorey algal species; TSM, a turf algae-sediment matrix assemblage, and; Turf, a turf algae assemblage with entrained sediments largely removed by flushing with water. Replicates in each treatment are $n = 5$, except for the TSM treatment where $n = 4$. Note the different y-axis scales.

Table 5.1 Results of 1-way fixed effects ANOVAs on biological response variables across the macroalgae assemblages – response variable (Y) and associated transformation is noted in the first column. Experimental treatments are 'Control' (a bare paver); 'Kelp', an algal assemblage dominated by the kelp *Ecklonia radiata*; 'US', an assemblage of understorey algal species; 'TSM', a turf algal-sediment matrix assemblage, and; 'Turf', a turf algae assemblage with entrained sediments largely removed by flushing with water. Note that for analyses of kelp recruitment and accumulated sediments in the field, the TSM and Turf pavers were functionally identical, since the Turf treatment could only be established in the lab. Outcomes of post-hoc *a priori* comparison tests are noted where the overall ANOVA was significant. Significant tests are in bold and with an asterisk.

data analysed	*F-value*	*P-value*	*post-hoc comparison tests*
Recruitment @ 50 days $(Y + 0.1)^{0.35}$	$F_{(3,16)} = 0.669$	0.583	
Recruitment @ 148 days $(Y + 0.1)$	$F_{(3,16)} = 3.894$	**0.029***	TSM vs Kelp: P = **0.046*** TSM vs US: P = 0.896 TSM vs Turf: P = 0.896
Recruitment @ 260 days $(Y + 0.1)^{0.5}$	$F_{(3,16)} = 4.234$	**0.022***	TSM vs Kelp: P = **0.013*** TSM vs US: P = 0.683 TSM vs Turf: P = 0.938
Biomass – total $(Y)^{0.5}$	$F_{(3,15)} = 64.328$	**<0.001***	TSM vs Kelp: P < **0.001*** TSM vs US: P < **0.001*** TSM vs Turf: P = 0.686
Biomass – turf algae $(Y + 0.0005)^{-0.2}$	$F_{(3,15)} = 17.824$	**<0.001***	TSM vs Kelp: P < **0.001*** TSM vs US: P < **0.001*** TSM vs Turf: P = **0.049***
Depth of accumulated sediments $(Y)^{0.2}$	$F_{(3,16)} = 13.181$	**<0.001***	TSM vs Kelp: P < **0.001*** TSM vs US: P = **0.019*** TSM vs Turf: P = 0.848

Table 5.2 Results of 1-way fixed effects ANOVA on O_2 profile parameters and water velocity across experimental treatments – response variable (Y) and associated transformation is noted in the first column as fixed factor. Experimental treatments are 'Control' (a bare paver); 'Kelp', an algal assemblage dominated by the kelp *Ecklonia radiata*; 'US', an assemblage of understorey algal species; 'TSM', a turf algal-sediment matrix assemblage, and; 'Turf', a turf algae assemblage with entrained sediments largely removed by flushing with water. 'Exp' denotes when all experimental assemblages were simultaneously tested against the Control treatment, and 'UPS' denotes the measurement of water velocity in the flume upstream of the macroalgae assemblages. Outcomes of post-hoc *a priori* comparison tests (O_2 profile parameters) and Tukey's Honest Significant Difference (water velocity) are noted. Significant tests are in bold and with an asterisk.

data analysed	*F-value*	*P-value*	*post-hoc comparison tests*
Difference at 0.0 mm $(Y)^{-3.35}$	$F_{(4,19)} = 15.365$	**<0.001***	TSM vs Kelp: P = **0.027*** TSM vs US: P = 0.162 TSM vs Turf: P = 0.999 Control vs Exp: P < **0.001***
Change in mainstream water $(Y)^{0.5}$	$F_{(4,19)} = 30.760$	**<0.001***	TSM vs Kelp: P < **0.001*** TSM vs US: P = **0.001*** TSM vs Turf: P = 0.357 Control vs Exp: P < **0.001***
Downstream water velocity $(Y)^{1.2}$	$F_{(4,3268)} = 1599$	**<0.001***	Kelp < US < TSM < Con = UPS

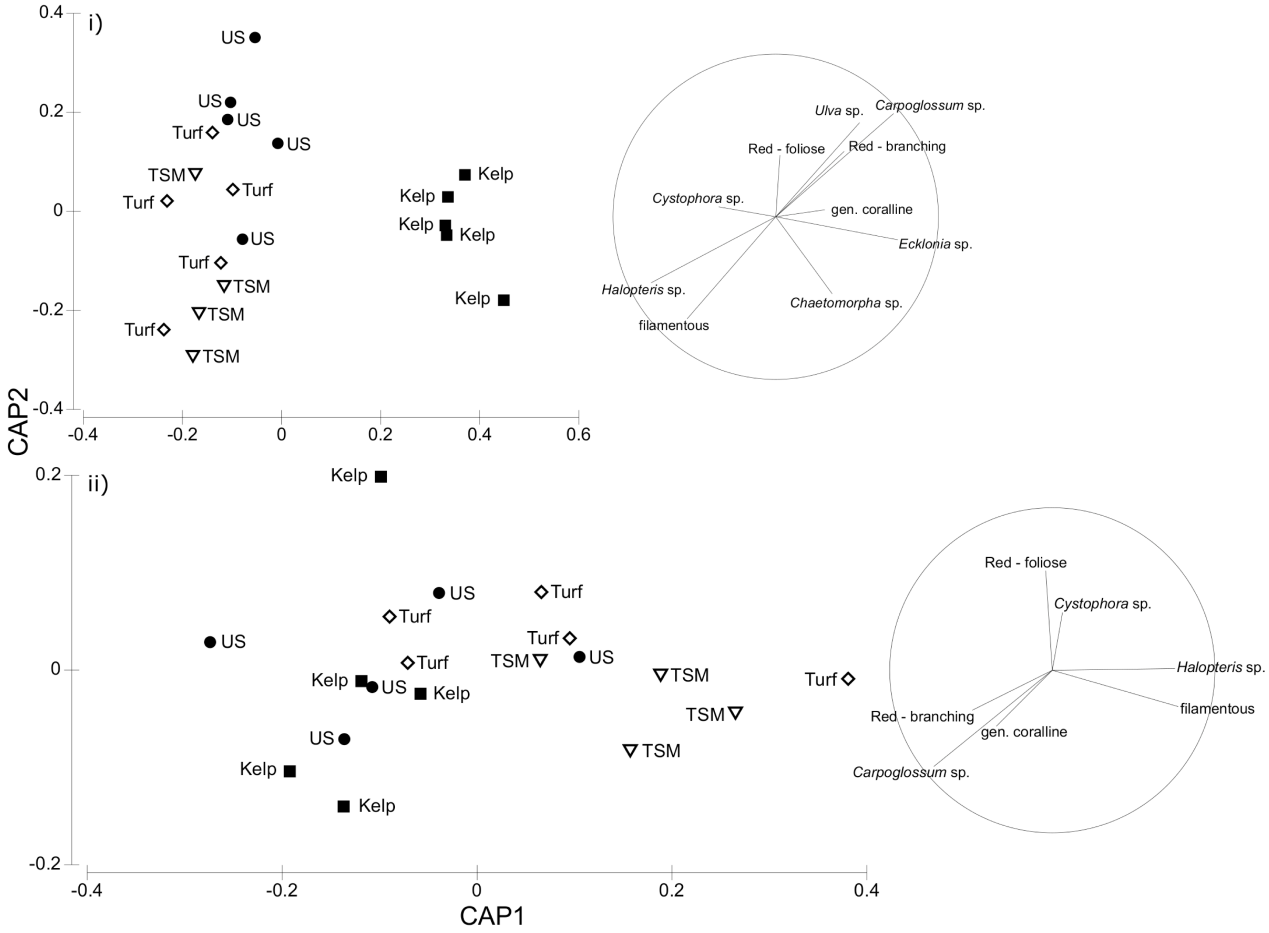

Figure 5.3 Canonical Analysis of Principle coordinates (CAP) of macroalgae assemblages using algal biomass from four experimental treatments. Vector plots illustrate principle macroalga driving assemblage differentiation. Fig. 5.3i is with full data, 5.3ii is with *Ecklonia radiata* and *Ulva* sp. excluded. Experimental treatments are Kelp, an algal assemblage dominated by the kelp *Ecklonia radiata*; US, an assemblage of understorey algal species; TSM, a turf algae-sediment matrix assemblage, and; Turf, a turf algae assemblage with entrained sediments largely removed by flushing with water. Note the different y-axis scales. Macroalga are identified by genus or functional group, and 'gen. coralline' denotes geniculate coralline algae. See Appendix 5.1 for taxonomic details.

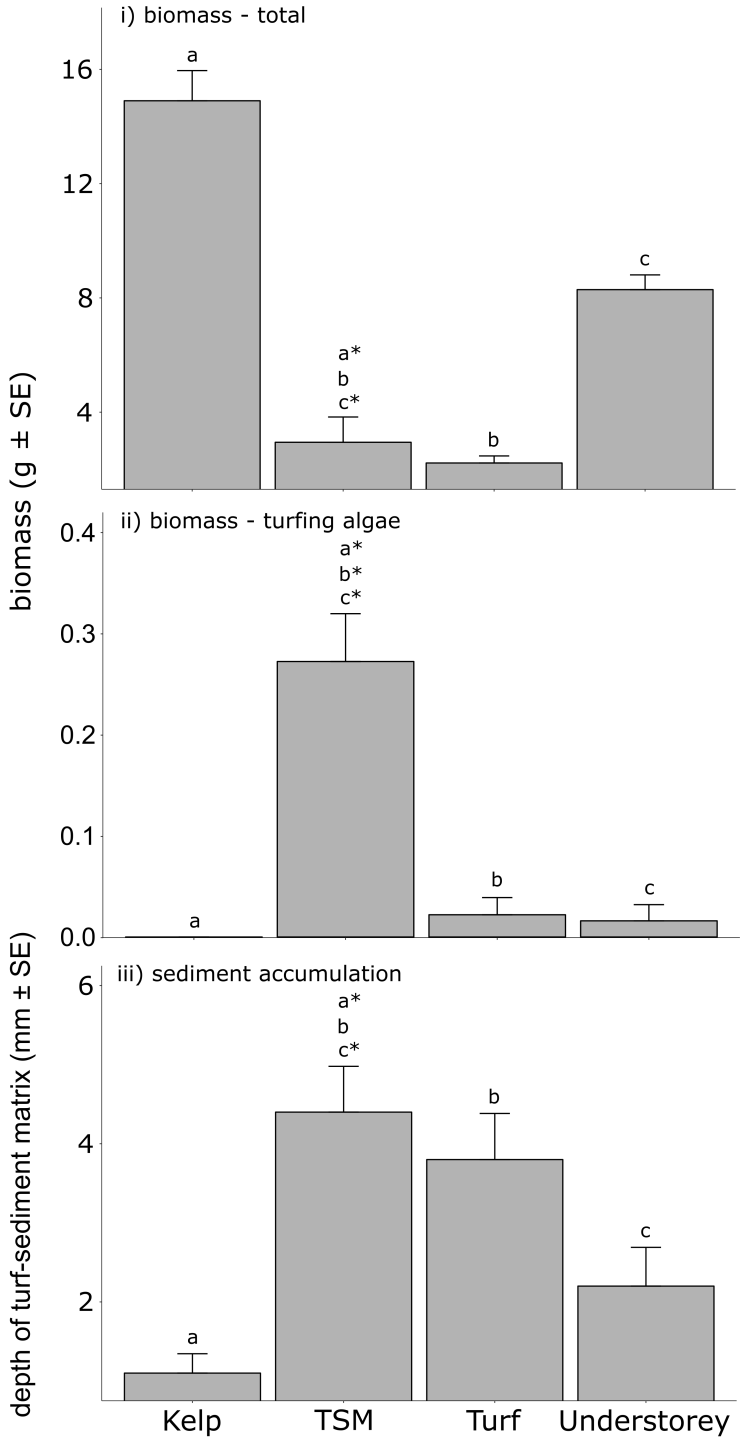

Figure 5.4 Mean (i) total macroalgae biomass, (ii) biomass of turf algae, and (iii) depth of accumulated sediments across four experimental macroalgae assemblages. Similar letters denote pairwise comparisons in post-hoc *a priori* comparison test, and an asterisk indicates significant pairwise differences (Table 5.1). Experimental treatments are Kelp, an algal assemblage dominated by the kelp *Ecklonia radiata*; Understorey, an assemblage of understorey algal species; TSM, a turf algae-sediment matrix assemblage, and; Turf, a turf algae assemblage with entrained sediments largely removed by flushing with water. Replicates in each treatment are $n = 5$, except for the TSM treatment where $n = 4$. Note the different y-axis scales.

Profiles of the macroalgal assemblages and water velocity

The starting mainstream value of O_2 concentration was 313 ± 5 µmol/L (SE, n = 24) and did not differ across treatments (ANOVA; $F_{(4,19)} = 0.910$, $P = 0.478$, Fig. 5.5). This equated to a pH of 7.99 ± 0.01. The bare sandstone Control pavers had little effect on seawater chemistry (Fig. 5.5), and there was no difference between start and finish values of mainstream O_2 concentrations during Control trials ($t_{(8)} = 0.370$, $P = 0.721$).

In contrast, the macroalgal assemblages exhibited elevated levels of O_2 concentration (and thus pH) throughout the vertical profiles (Fig. 5.5). O_2 concentration at the benthos, where it was typically highest, differed significantly between the four macroalgal assemblages and the Control (Fig. 5.5, Table 5.2). Across the macroalgal assemblages, O_2 concentration at the benthos differed between the Kelp and TSM treatments, but not other treatments. Mean ambient seawater parameters (~315 µmol O_2/L, pH ~7.99) were elevated to ~375 µmol O_2/L (pH ~8.10) at the benthos within the Kelp treatment, and to ~520 µmol O_2/L (pH ~8.35) within the TSM treatment, with maximum values in the latter >600 µmol O_2/L (pH ~8.50) (Fig. 5.5).

Changes to O_2 concentration profiles within the Kelp and Understorey assemblages were mostly gradual (Fig. 5.5). Within the Kelp assemblage, O_2 concentration initially had a decreasing trend above the benthos, with an increase of similar magnitude at distances >2 mm. Overall, there were no sharp alterations to O_2 concentration indicative of a benthic CBL, and no CBL was detected in the Kelp assemblage. The Understorey treatment also had a trend of decreasing O_2 concentration above the benthos but stabilised at >1 mm above the benthos. However, no CBL was detected in this treatment either. Overall, there were significant differences between the O_2 concentration profiles within the Understorey and Kelp treatments (Vuong closeness test; $w^2 = 0.301$, $P < 0.001$), possibly reflecting that at ~2.0 mm above the benthos, mean O_2 concentration declined in the Understorey treatment but increased in the Kelp treatment relative to values closer to the paver surface.

Within the two turf algae assemblages, very high O_2 concentrations at the benthos decreased rapidly and similarly within the first 0.4 mm above the benthos (Fig. 5.5). As the distance above the paver increased, the decline in O_2 concentration was greater in magnitude and duration within the Turf treatment without sediments. CBL thickness was 1.0 and 0.8 mm within the TSM and Turf treatments, respectively. The overall profiles of O_2 concentration within the two turf algae assemblages did not differ from one another (Vuong closeness test; $w^2 = 1.351$, $P = 0.500$).

Despite inducing less microscale alterations to O_2 concentration, the Kelp and Understorey treatments produced significantly greater changes to mainstream seawater than the turf assemblages (Fig. 5.6, Table 5.2). Nonetheless, the TSM and Turf treatments still altered mainstream O_2 concentration significantly more than the Control pavers.

The three unmodified macroalgal assemblages (Kelp, Understorey & TSM) all differed in their capacity to reduce water flow. Relative to the upstream water velocity, downstream water velocity was significantly reduced by the experimental treatments but not the bare Control paver (Fig. 5.7, Table 5.2), and was lowest downstream from the Kelp treatment, followed by the Understorey then TSM treatment.

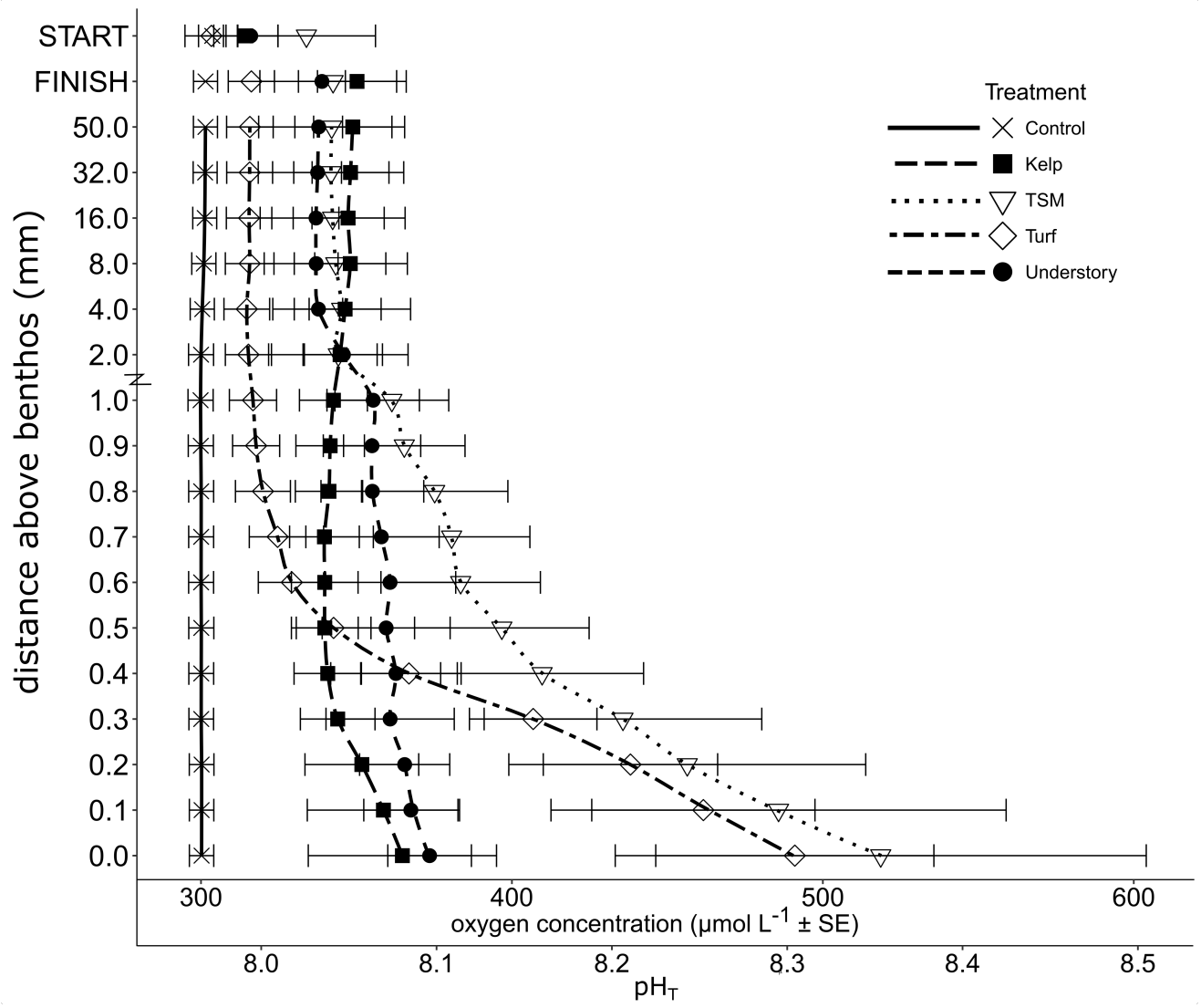

Figure 5.5 Mean oxygen concentration (µmol/L) and total pH (pH_T) profiles within four experimental macroalgae assemblages and a control. Experimental treatments are Control (a bare paver); Kelp, an algal assemblage dominated by the kelp *Ecklonia radiata*; Understorey, an assemblage of understorey algal species; TSM, a turf algae-sediment matrix assemblage, and; Turf, a turf algae assemblage with entrained sediments largely removed by flushing with water. Estimate of pH was derived from a linear relationship ($r^2 = 0.97$) between O_2 saturation and pH_T (Noisette & Hurd in press). Replicates in each treatment are $n = 5$, except for the TSM treatment where $n = 4$. Note y-axis scale is nonlinear, see axis break.

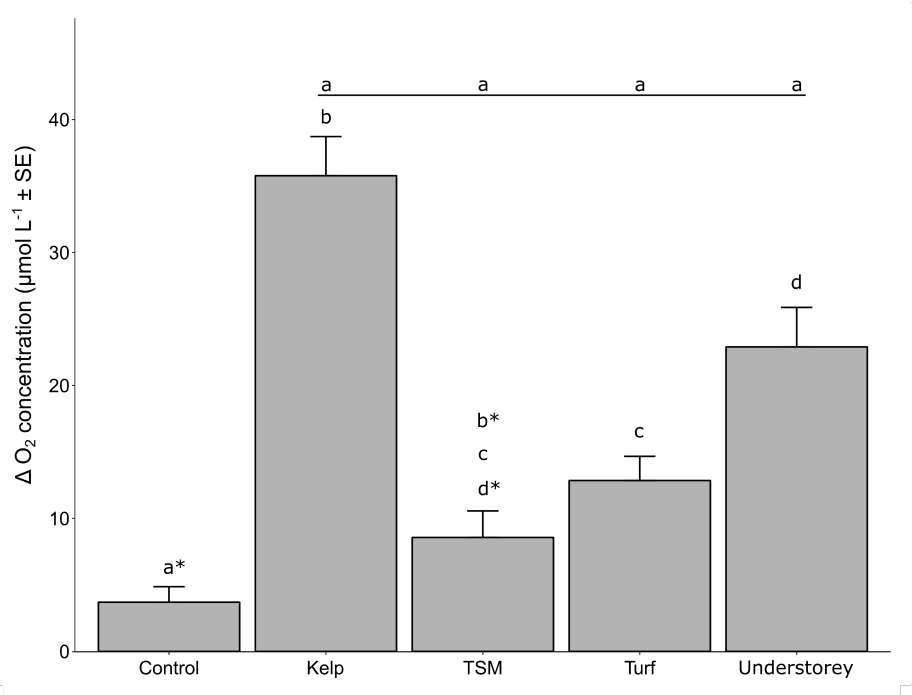

Figure 5.6 Mean change in O_2 concentration within mainstream seawater over the length of the trial across four experimental macroalgae assemblages. Outcomes of post-hoc *a priori* comparison tests are noted: similar letters identify the pairwise comparison and an asterisk indicates significant pairwise differences (Table 5.2). Experimental treatments are Control (a bare paver); Kelp, an algal assemblage dominated by the kelp *Ecklonia radiata*; Understorey, an assemblage of understorey algal species; TSM, a turf algal-sediment matrix assemblage, and; Turf, a turf algae assemblage with entrained sediments largely removed by flushing with water. Replicates in each treatment are $n = 5$, except for the TSM treatment where $n = 4$.

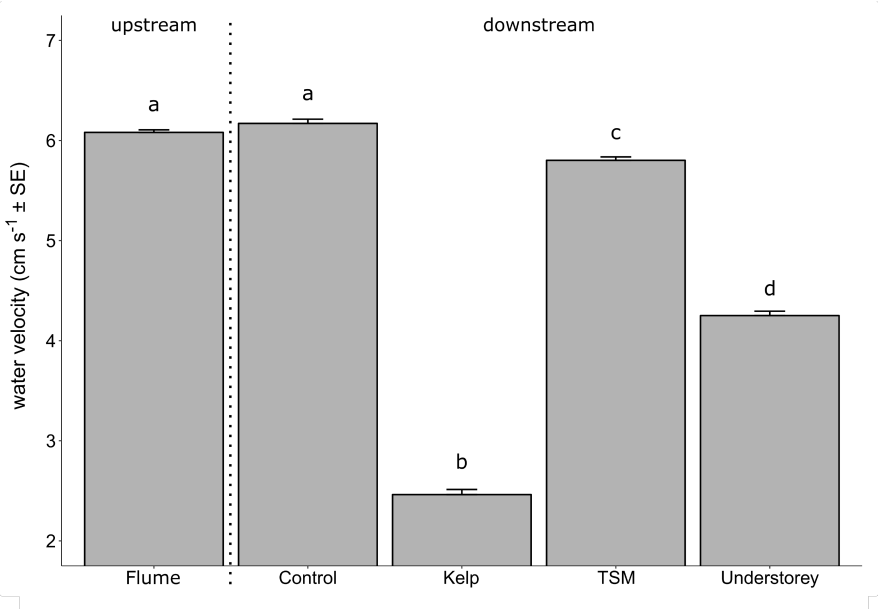

Figure 5.7 Mean upstream water velocity of the experimental flume relative to measurements taken downstream of the 3 unmodified macroalgal assemblages and control pavers. Letters a–d indicate Tukey groupings from Honest Significant Difference post-hoc tests. Experimental treatments are Control (a bare paver); Kelp, an algal assemblage dominated by the kelp *Ecklonia radiata*; Understorey, an assemblage of understorey algal species; TSM, a turf algal-sediment matrix assemblage. Data represent the mean of 600 measurements recorded over 60 seconds.

Discussion

We illustrate that the chemical environments within macroalgal assemblages is characterised by elevated O_2 concentrations and pH relative the surrounding seawater. Moreover, these parameters were significantly higher at the benthos within a turf-sediment matrix assemblage than in a kelp-dominated assemblage that contained little turf algae. There was little distinction however between microenvironments within natural turf assemblages with entrained sediments and turf assemblages with most of the sediments removed – indicating that the responses we observed were due to the turf algae rather than any effect of sediments. Differences in O_2 concentration and pH within macroalgal assemblages may have implications for the recruitment of kelp into these environments. Certainly, during the development of the assemblages in the field, the recruitment of kelp was significantly greater in the kelp-dominated assemblage than in treatments supporting dense turf algae.

Community structure of experimental assemblages

Previous studies have obtained microscale profiles of macroalgal assemblages comprising only one or two species (Cornwall et al. 2013, 2015), while our naturally-developed macroalgal assemblages contained up to six taxa and/or multispecies functional groups (Appendix 5.1). CAP confirmed the distinct community identity of the experimental assemblages at the time of profiling, clearly differentiating those treatments with and without kelp. The assemblages were distinctive (albeit to a lesser extent) even without the presence of the canopy-forming kelp or a dominant understorey species. Thus, despite developing under consistent environmental conditions (i.e. depth, exposure, proximity to the adult kelp canopy), the presence/absence of *Ecklonia radiata* and *Ulva* sp. on the pavers led to community-level differences. This illustrates the influence of kelp and some understorey algae in shaping the composition of the associated community, even when the macroalga are relatively small and the communities are not fully developed (also see Smale et al. 2011).

The key drivers of community differentiation we observed (Fig. 5.3) are consistent with associations observed in many temperate reef communities; in which fleshy and foliose red and coralline algae typically occur beneath kelp canopies (Dayton et al. 1984; Irving & Connell 2006), and filamentous turf algae in areas free of canopy-forming species (Kennelly 1987; Irving & Connell 2006). These 'assembly rules' (*sensu* Irving & Connell 2006) manifest due to modification of sub-canopy conditions by the kelp, including reduced irradiance (benefitting red algae) and increased physical abrasion of the benthos (inhibiting turf algae) (Dayton et al.1984; Irving & Connell 2006; Chapters 2 & 4).

Overall, the modifications of seawater carbonate chemistry that we observed within the experimental assemblages – from pH 7.99 to ~8.50 – were greater than previously detected in two-species assemblages assessed under similar flow and irradiance (pH ~8.0 to <8.3, Cornwall et al.

2015). This illustrates the strength of the observed response and the utility of examining macroalgal assemblages that are as similar as possible to those in the field.

Altered pH and O_2 concentration at microscales

Photosynthesis by the macroalgae modified the chemical microenvironment within the assemblages relative to ambient conditions. The most highly modified conditions occurred at the surface of the benthos and differed significantly between the kelp-dominated and turf algae assemblage – which respectively, had the lowest and highest concentrations of O_2 and pH. The kelp and turf algae assemblages also clearly differed in the magnitude and duration of chemical modification across their profiles (Fig. 5.5). Evidently, total algal biomass was not an accurate predictor of elevated O_2 or pH within the experimental assemblages. Nor was the biomass of turf algae in each treatment an accurate predictor, and despite slight but significant differences in turf algae biomass, the two turf algae treatments had very similar profiles (Fig. 5.5).

Subsequently, physical characteristics of the macroalgal assemblages might mediate the modifications to seawater chemistry caused by photosynthesis. For example, the complex matrices formed by turf algae assemblages are likely to effectively retain water, promote CBL formation and inhibit diffusion of the metabolic by-products into the ambient seawater (Hay 1981; Pöhn et al. 2001; Cornwall et al. 2014). Indeed, dense turf-forming assemblages restrict water exchange more than canopy-forming algae (Hauri et al. 2010), suggesting less 'refreshing' of the chemical environment within turf assemblages (Hay 1981). Thus, the physical morphology of the turf assemblage likely contributed to the dramatic microscale alterations to ambient conditions that we observed.

Certainly, turf algae matrices are very effective at trapping sediments, even when sparse (Stewart 1983; Kendrick 1991) and we detected far more sediments within turf algae assemblages than the others (Fig. 5.4). Although, given the similar profiles from the two turf algae treatments (Fig. 5.5) – one of which contained no sediments – it seems sediments did not contribute to the elevated levels of O_2 and pH we observed.

Filamentous turf algae also possess greater surface-to-volume ratios than the larger kelp and understorey algae, leading to higher mass-specific productivity (Copertino et al. 2005; Miller et al. 2009) and likely greater diffusion of O_2 into the water volume. However, this too is likely to be mediated by physical characteristics of the assemblages. In the Understorey treatment, shading of the turf by the sub-canopy of understory algae would reduce turf algae productivity and thus modification of the seawater caused by their photosynthetic activity (Hay 1981; Miller et al. 2009; Cornwall et al. 2015). This may explain why the Turf and Understorey treatments had such dissimilar profiles (Fig. 5.5) despite possessing similar biomass of turf algae (Fig. 5.4). Equally, negligible shading of the turf algae in the two turf treatments could explain why they had such similar profiles, despite containing

different biomass of turf algae. Shading of the lower strata of understorey alga by the kelp canopy (Wernberg et al. 2005; Chapters 2 & 4) is consistent with the kelp-dominated assemblage showing the least modified benthic microenvironment.

Thus, while metabolic activity is responsible for altering seawater chemistry within the macroalgal assemblages, interactions with abiotic factors appear capable of mediating the magnitude of the response. Some factors such as irradiance directly influence productivity and photosynthesis, while others such as assemblage morphology may influence retention of metabolites within the CBL.

Water velocity and Concentration Boundary Layers (CBL)

Unlike the modifications to seawater chemistry, reductions in water velocity in the flume were closely related to the biomass of the assemblages (Figs. 5.3, 5.6). Reductions in mainstream seawater velocity by the assemblages are likely to equate to similar reductions in water velocity within the assemblages that extend to the benthos (Kregting et al. 2011; Cornwall et al. 2015). Due to logistical constraints, we were unable to explore this effect and so consider our measurements as broad estimates of the relative flow-reducing capacity of these assemblages. No less, our measure of flow-reduction by the kelp assemblage (~ 59%) is similar to those previously reported beneath stipitate kelp canopies (50–58% reductions, Eckman et al. 1989; 55% reductions, Chapter 4).

The natural complexity and variability of the experimental assemblages made it difficult to detect well-defined and consistent CBLs, especially in the Understorey and Kelp treatments where there were likely multiple sub-canopy layers (Miller et al. 2009; Cornwall et al. 2013). Accordingly, this sub-canopy structure will have contributed to the formation of additional small CBLs within the algae assemblages (Cornwall et al. 2015; Hurd 2015). The presence of one of these small CBLs may be noticeable in the Understorey treatment 2–4 mm above the benthos (Fig. 5.5).

It is likely that the CBL of the Understorey and Kelp treatments extended even further than 50mm from the benthos (Frieder et al. 2012; Britton et al. 2016), which was the greatest vertical distance we could profile accurately. The profiles from within the Kelp and Understorey treatments must therefore be entirely within a canopy boundary layer, which may explain the relative stability of the profiles (Fig. 5.5). The turf algae assemblages were structurally simpler, and CBL thickness was 0.8–1 mm in these assemblages. This is comparable to previously reported values of CBL thickness from a coralline turf assemblage (0.2–0.7 mm, Cornwall et al. 2015) – especially considering the higher water velocity used by Cornwall and colleagues (8 vs 6 cm/sec used here).

Thus, the relatively small volume of modified seawater within turf algae matrices (i.e. the CBL) may be susceptible to large and rapid fluctuations between hyperoxia (as we demonstrate) and anoxia (due to respiration, Pöhn et al. 2001; Hauri et al. 2015; Cornwall et al. 2015). On the contrary, the larger volume of modified seawater within the (sub)canopy of kelp and understorey assemblages

may facilitate greater environmental stability, even despite the greater capacity of these assemblages to modify mainstream seawater (Fig. 5.6; Britton et al. 2016). Ultimately, while the highly modified environments within turf assemblages typically occur at very fine scales right at the benthos, this is ample space for interactions to occur with other microscopic processes, such as the settlement and recruitment of kelp propagules.

Patterns and potential mechanisms of kelp recruitment inhibition

Once the distinct experimental assemblages had become established in the field, there was significantly greater recruitment of *E. radiata* in the kelp-dominated community than in the other macroalgal communities (Fig. 5.2). The minimal recruitment of *E. radiata* throughout the final sampling period in late spring and summer and across all treatments is consistent with seasonal patterns of recruitment in *E. radiata* (Kirkman 1981; Chapter 3).

Our observations complement existing knowledge of the inhibition of kelp recruitment (and specifically, *E. radiata*) by turf algae (Kennelly 1987; Valentine & Johnson 2005; Strain et al. 2014; Filbee-Dexter & Wernberg 2018). Recent work suggests understorey algae may also impair *E. radiata* recruitment (Tatsumi & Wright 2016), although the understorey algae present in the Kelp treatment (Appendix 5.1) did not appear to elicit this same response (Fig. 5.2). This suggests that turf algae and sediments within these assemblages may be the primary inhibitor, rather than the foliose understorey algae themselves. The Understorey treatment did contain more sediments and turf algae than the kelp-dominated assemblage (Fig. 5.4), and also a significantly different O_2 profile. Thus, while it is well established that turf algae inhibit recruitment of kelp, it is less clear whether the high O_2 concentrations and pH we observed within the turf communities inhibit kelp recruitment, and equally, whether turf algae are less inhibited (or benefit) under these same conditions.

The spores and gametophytes of two species of kelp, *Macrocystic pyrifera* and *Undaria pinnatifida*, have been shown to have better rates of germination, growth and development under lower pH (7.20–7.65) than higher pH (8.01–8.40) (Roleda et al. 2012; Leal et al. 2017). This is likely due to a higher concentration of DIC at lower pH (especially CO_2), which is necessary for photosynthesis (Leal et al. 2017; Hurd et al. 2014). DIC can be a limiting resource in macroalgal photosynthesis, especially in environments of high productivity (Kregting et al. 2011) or for species without the capacity to utilise multiple forms of carbon found in seawater (Giordano et al. 2005; Hurd et al. 2014). Because macroalgae employ various carbon uptake strategies, it is possible that turf algae are not equally impaired by high pH and can more efficiently utilise the limited DIC available under such conditions (Giordano et al. 2005; Hepburn et al. 2011; Connell et al. 2013). Unfortunately, the carbon uptake strategies of *E. radiata* and the turf algae assemblage studied herein are still unclear and may even change between different life stages (Zhang et al. 2006).

Nonetheless, there is evidence that differences in carbon uptake strategy can confer a competitive advantage for macroalgae. Björk et al. (2004) demonstrate that photosynthesis by *Ulva intestinalis* can dramatically elevate the pH in rock pools up to pH 10, at which point CO_2 concentrations are undetectable and bicarbonate also very low. These conditions provide a competitive advantage for *U. intestinalis* by inhibiting the presence of other normally co-occurring species of macroalgae. This is suggested to be due to species-differences in carbon uptake efficiency (also see Hepburn et al. 2011), with *U. intestinalis* capable of maintaining higher rates of photosynthesis relative the other species in the high pH/low DIC environments. This may also explain why *Ulva* spp. are some of the few macroalgae that occur in turf algae habitats in Australia (pers. obs.). Whilst pH 10 is well above the levels we detected, we did observe levels of pH within the turf assemblages that are known to impair the growth and photosynthesis of some brown and red macroalgae (Middelboe & Hansen 2007). Intriguingly, the impaired functions of these macroalgae persisted even when the high pH levels were manipulated to not cause the usual reductions in DIC. Thus, it seems likely there are additional factors involved.

Highly concentrated levels of O_2, like those observed in the turf assemblages, can also be detrimental for macroalgal photosynthesis. This is because O_2 competes with CO_2 as the binding substrate for RUBISCO – a key enzyme in the photosynthetic pathway (Giordano et al. 2005). Binding of O_2 to RUBISCO is referred to as photorespiration and, compared to the binding of CO_2 (i.e. photosynthesis), it is a less efficient process for production of energy (Giordano et al. 2005; Buapet et al. 2013). Certainly, increased concentrations of O_2 can cause photorespiration and reductions in photosynthetic efficiency in macroalgae (Gordon & Sand-Jensen 1990; Mass et al. 2010). However, some species of macroalgae are more prone to photorespiration than others (c.f. Buapet et al. 2013), indicating the potential for competitive advantages under high O_2 conditions. It follows that differences between RUBISCO activity in kelp and turf algae may therefore result in disparate responses to the elevated concentrations of O_2 present within the turf assemblages (Jordon & Odren 1981; Hurd et al. 2014).

We require a better understanding of the ecophysiology of the study species to determine whether carbon limitation or photorespiration is responsible for inhibition of kelp recruitment by turf algae assemblages. Other physio-chemical interactions might also contribute to this phenomenon, including interspecific differences in, the activity and efficiency of photosynthetic pigments (Wood 1987; Hurd et al. 2014), or inter-cellular pH regulation and membrane processes (Middelboe & Hansen 2007; Roleda et al. 2012). However, these remain even less well understood for the study species.

Feedbacks, alternative stable states and future ocean conditions

The replacement of kelp habitats with turf algae is a substantial ecological and economic problem in many places globally (Steneck & Johnson 2014; Strain et al. 2014; Filbee-Dexter & Wernberg 2018). Key concerns are, the suddenness with which kelp-dominated habitats can phase shift and become dominated by turf algae, and that hysteresis in the system can make it very difficult to push the ecosystem back to the desired kelp state – even with external intervention (Valentine & Johnson 2005; Gorman & Connell 2009; Johnson et al. 2017). Chemical modifications of the benthic microenvironment by turf algae may represent a previously unknown pathway that enables both these dynamics to occur. This is because the modified chemical microenvironment might not only inhibit kelp recruitment but, in doing so, also facilitate the formation of more turf algae, thus reinforcing the original inhibition of kelp. This runaway positive feedback would result in accelerating-impacts and strong hysteresis in system (Marzloff et al. 2011; Steneck & Johnson 2014; Filbee-Dexter & Wernberg 2018). The role of positive feedbacks in influencing habitat dynamics are gaining greater attention (see Bulleri 2009; Marzloff et al. 2011; Bennett & Wernberg 2014). Indeed, we suggest that a similar positive feedback cycle is a powerful mechanism contributing to stability of *E. radiata* kelp habitats (Chapter 4).

Critically, ocean warming and acidification may alter the dynamics between these alternative stable states by stimulating the growth and persistence of turf algae (Connell et al. 2013; Falkenberg et al. 2015) and impairing growth of juvenile kelp (Mabin et al. 2013; Britton et al. 2016). The overall effect being that the ecosystem dynamic becomes skewed towards a state more inherently suitable for turf algae than kelp (Johnson & Connell in prep.). This may explain the dominance of turf algae over kelp and other canopy-forming macroalgae observed in simulated future-ocean mesocosms (Connell et al. 2013; Falkenberg et al. 2015) and at natural CO_2 vent systems (Porzio et al. 2013).

Conclusions

We present initial analyses of the microenvironment within natural and complex multispecies macroalgal assemblages, demonstrating that metabolic processes modify seawater chemistry at micro-spatial scales within these assemblages. Crucially, the chemical microenvironment within turf algae assemblages is characterised by significantly higher concentrations of O_2 and pH relative to kelp assemblages, likely due to less shading of the highly productive turf algae and less refreshing of the modified water volume within the turf matrix. These differences may explain the widely recognised phenomena of the inhibition of kelp recruitment by turf algae – a pattern we also observed during field observations of the experimental assemblages. Although more work on the ecophysiology of kelp (particularly the microscopic stages) and turf algae is necessary before identifying any potential mechanisms of inhibition. All of this reinforces our knowledge that degradation of kelp habitats can

result in proliferation of turf algae habitats and persistent localised absences of kelp. The successful re-establishment of which may require external intervention such as ecosystem restoration.

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Appendices

Appendix 5.1 Algal biomass (g dry weight) within experimental assemblages. Alga were identified to species-level where possible but otherwise according to genus or functional group. Experimental treatments are 'Kelp', an algal assemblage dominated by the kelp *Ecklonia radiata*; 'US', an assemblage of understorey algal species; 'TSM', a turf algal-sediment matrix assemblage, and; 'Turf', a turf algae assemblage with entrained sediments largely removed by flushing with water. Replicates (#*X*) in each treatment are $n = 5$, except for the TSM treatment where $n = 4$.

	Kelp #1	**Kelp #2**	**Kelp #3**	**Kelp #4**	**Kelp #5**	**TSM #1**	**TSM #2**	**TSM #4**	**TSM #5**	**Turf #1**	**Turf #2**	**Turf #3**	**Turf #4**	**Turf #5**	**US #1**	**US #2**	**US #3**	**US #4**	**US #5**
Carpoglossum confluens	0.290	0.000	0.820	0.440	0.310	0.020	0.005	0.080	0.260	0.000	0.005	0.005	0.080	0.210	0.740	0.030	0.390	0.005	0.600
Carpomitra costata	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000
Chaetomorpha sp.	0.000	0.005	0.005	0.100	0.340	0.005	0.050	0.000	0.020	0.000	0.000	0.005	0.005	0.000	0.000	0.130	0.070	0.000	0.000
Cystophora sp.	0.000	0.005	0.000	0.005	0.000	0.005	0.120	0.210	0.000	0.000	0.040	0.000	0.005	0.005	0.005	0.005	0.000	0.000	0.010
Ecklonia radiata	7.170	9.040	0.860	7.690	9.710	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Filamentous alga	0.000	0.000	0.000	0.000	0.000	0.270	0.140	0.005	0.350	0.090	0.005	0.005	0.005	0.005	0.000	0.080	0.000	0.000	0.000
Geniculate coralline alga	0.000	0.000	0.090	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Halopteris paniculata	0.005	0.000	0.000	0.005	0.090	0.080	0.290	0.070	0.040	0.100	0.330	0.060	0.005	0.130	0.005	0.040	0.010	0.005	0.000
Red alga - branching	0.030	0.000	0.000	0.005	0.170	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.110	0.000	0.000	0.005	0.000	0.080
Red alga - foliose	0.000	0.040	0.000	0.010	0.100	0.005	0.000	0.150	0.005	0.005	0.050	0.010	0.040	0.080	0.000	0.160	0.060	0.100	0.360
Ulva sp.	9.260	4.050	9.840	8.170	5.820	1.420	1.100	4.980	2.100	1.340	1.750	1.860	2.300	2.470	6.170	7.520	8.070	9.940	6.830

Chapter 6. General Discussion

Some of the earliest ecological research focussed on kelp forests (Kitching et al. 1934; Kitching 1937, 1941). Kitching and colleagues were also pioneers of scientific diving and, wearing a modified milk can as a diving helmet and breathing via a length of garden hose connected to a foot-pump (which required constant operation by a willing student), some of the team's earliest work described the light and sediment conditions beneath kelp canopies (Kitching et al. 1934). Scientific diving has certainly progressed since then, but almost 85 years later similar research questions still require answering – now within the context of an established foundation of ecological theory and a planet that is under ever-increasing stress from human activity.

The central thesis presented here is that modification of the sub-canopy environment by the kelp *Ecklonia radiata* facilitates the survival and development of juvenile conspecifics beneath the adult canopy. However, when *E. radiata* habitats are degraded (e.g. by anthropogenic sources), this positive feedback is reduced or breaks down completely because the capacity of the kelp canopy to engineer the environment is impaired by the reductions to patch size and adult kelp density. In turn, this leads to disruption and even collapse of the demographic processes of micro- and macroscopic juvenile *E. radiata* and ultimately, a loss of stability and resilience.

The specific mechanism(s) responsible for disrupting the settlement, recruitment, survivorship and growth of micro- and macroscopic juvenile *E. radiata* in the absence of sufficient adult conspecifics remain to be identified. It seems likely that there is no single causative factor however, and that rather multiple factors disturb and stress the micro- and macroscopic life stages. Sedimentation in particular is likely a significant stressor to the settlement and development of the microscopic life stages (Chapters 2, 3, 4, 5) due to smothering, abrasion and substratum instability (Devinny & Volse 1978; Airoldi 2003; Geange et al. 2014; Watanabe et al. 2016). These effects might also be exacerbated by high light stress and the altered hydrodynamics (Chapters 2 & 4) and chemical microenvironments (Chapter 5) in degraded sub-canopy environments, which can negatively influence propagule settlement and development (Eckman et al. 1989; Serrão et al. 1996; Graham 2003; Cie & Edwards 2006). Sedimentation and altered chemical microenvironments are less likely to pose significant threats to established macroscopic juvenile kelp. Nonetheless, larger sporophytes may suffer cumulative impacts from a variety of sub-lethal stressors in the degraded sub-canopy environment, such as deleteriously high irradiance (Wood 1987; Chapters 1 & 3) and water flow (Eckman et al. 1989; Chapters 1 & 3), herbivory (Velimirov & Griffiths 1979; Kriegisch et al. 2016) and/or epiphytism (Fletcher & Day 1983).

Niche space and stress amelioration

Kirkman (1981) first discussed the array of circumstances necessary for juvenile *E. radiata* to recruit and survive, describing the locations where these requirements are fulfilled as 'safe sites' – a term coined by Harper et al. (1961) in their work on the ecology of sympatric plant species. Kirkman defines safe sites for *E. radiata* as locations with appropriate substratum for attachment, access to resources such as light and nutrients and crucially, free from physical stressors (e.g. sediments) and disturbances (e.g. dislodgement). Dayton et al (1984) emphasised similar complexities in their work with *Macrocystis pyrifera*, stating that once dispersal and fertilisation has occurred, survival is determined "by the precise location of the propagule settlement" and by fine scale variations in light, nutrients, scour, and herbivory (see also Reed 1990a). Essentially, engineering by adult *E. radiata* seems to increase availability of these safe sites for juvenile conspecifics through provisioning of suitable habitat and amelioration of physical stressors. In doing so, this intraspecific facilitation seems to expand the 'realised niche' of the juvenile *E. radiata.*

Hutchinson's seminal discussion of niche theory (Hutchinson 1957) – notably, made in the closing remarks of some symposium proceedings – posits that the suite of abiotic requirements that determines where organisms live defines their 'fundamental niche'. For *E. radiata* and other kelp, these requirements might include suitable levels of light, temperature, nutrients, and water motion. Hutchinson explains further however that the fundamental niche is mediated through biotic interactions (e.g. competition, predation), such that species are typically distributed within a narrower range of conditions and environments than their physiology allows – and thus creating the 'realised niche'. However, it seems that by allowing juveniles to thrive in areas where they would otherwise perish in isolation, engineering by adult *E. radiata* expands the realised niche of juvenile conspecifics beyond their fundamental niche.

Bruno et al. (2003) theoretically predicted this somewhat paradoxical phenomenon during their incorporation of facilitation theory with niche theory. Nonetheless, this remains a topic of some contention, based mostly around the definition of a niche as either a physical or conceptual construct (see Stachowicz 2012; Bulleri et al. 2016). Following the former definition, stress amelioration from interspecific facilitation has been shown to expand the realised niche of organisms beyond their fundamental niches in intertidal (Silliman et al. 2011) and salt-marsh (Crotty & Bertness 2015) habitats. However, here I provide a rare empirical example of niche space expansion via intraspecific facilitation (reviewed by Buller et al. 2016; also see Loayza et al. 2017).

Stress gradients

Considering the role of stress amelioration in the positive environment-engineer feedback, the importance of intraspecific facilitation of juvenile *E. radiata* might strengthen in increasingly stressful

environments. This fits with the Stress Gradient Hypothesis, which posits that the frequency and importance of facilitation will increase along a gradient of increasing abiotic stress (Bertness & Callaway 1994; Crain & Bertness 2006).

In subtidal environments, many gradients of abiotic stress are likely to be intrinsically linked to the depth-attenuation of potential stressors such as irradiance (e.g. Wood 1987), wave exposure (e.g. Kitching 1941) or ice scour (e.g. Chapman & Johnson 1990). On the deeper reefs studied in Chapters 2 and 3 (at 14 m depth), the positive effects of patch size (and thus adult presence) on the demography of juvenile *E. radiata* were weaker and less consistent relative to the shallower reefs in Chapter 4 (6.5 m depth). This may reflect that due to the exponentially lower levels of ambient irradiance there was less potential for light stress (Wood 1987) and less potential for formation of deleterious turf-sediment matrices (Copertino et al. 2006; Miller et al. 2009) – even in the absence of engineering of the local environment from the adult canopy.

As an approximate comparison, mean ambient irradiance – measured at midday during spring – was 153 ± 4 µmol photon m^{-2} s^{-1} (n = 40, with a maximum of 236 µmol photon m^{-2} sec^{-1}) at the deeper site (14 m) and 558 ± 26 µmol photon m^{-2} sec^{-1} (n = 112, with a maximum of 1417 µmol photon m^{-2} sec^{-1}) at the shallower (6.5 m) site. Likewise, a light extinction coefficient of k = -0.226, calculated for waters nearby the shallower field site (Johnson & Swadling unpubl.), reveals that while 23% of surface irradiance penetrates to 6.5 m depth, only 4% reaches to 14 m. This is similar to data presented by Wood (1987) from Western Australia, illustrating that nearly 30% of surface irradiance during summer penetrates to reefs at 5 m depth.

Accordingly, the results from Chapters 2 and 4 hints that facilitation of juvenile *E. radiata* by the adult canopy might be more important in shallower, more stressful environments. These chapters also illustrate the potential complexity of environment-engineer feedbacks, with an abiotic stressor (i.e. sedimentation) manifesting via a biotic pathway (i.e. formation of turf algae) that is moderated by abiotic engineering (i.e. shading and scour) from the physical structure (i.e. the kelp canopy).

Gradients of abiotic stress in subtidal environments can also occur across latitude, due to changes in water temperature and irradiance. Previous work suggests that facilitation of juvenile *E. radiata* by the adult canopy is more important at lower latitudes in Western Australia, where water temperatures are higher and thermal stress is greater (Wernberg et al. 2010, 2011). The mechanisms of facilitation were not investigated by Wernberg and colleagues, but they propose that thermal stress increases the overall sensitivity of juvenile *E. radiata* to sub-lethal stressors (e.g. disease, light stress, grazing) that might otherwise be ameliorated by the adult canopy.

The implication of these observations is that populations of *E. radiata* in deeper locations and/or at higher latitudes may possess greater inherent resilience than those in shallower/lower

latitude locations. This is because the more benign levels of abiotic stress necessitate that less facilitation is required for development and survival of juvenile life stages.

Interestingly, the subtidal is not classically considered as a physically stressful environment, especially compared to intertidal environments (Bertness & Callaway 1994; Witman & Dayton 2001; Holmgren & Scheffer 2010). For this reason, facilitation theory posits that stress amelioration will be uncommon in subtidal environments, and that instead, associational defence (i.e. associations that alleviate predation/herbivory) will be the predominant mechanism of facilitation (Bruno et al. 2003; Crain & Bertness 2006; Bulleri 2009).

Ecosystem engineering by kelp can certainly influence herbivory, where scour and sweeping of the kelp can exclude herbivores from the sub-canopy (Velimirov & Griffiths 1979; Konar & Estes 2003). However, the effects of herbivores on the field experiments conducted here were expected to be minimal considering there was low/no abundance of macrograzers at the field sites. This occurred because the predominant kelp-grazing fish *Olisthops cyanomelas* (formerly *Odax cyanomelas,* see Andrew & Jones 1990) is not abundant in south-eastern Tasmania where the field sites were located, and also because I purposefully removed *Centrostephanus rodgersii* urchins from the experimental patches in Chapters 2 and 3 to avoid impacts from their destructive overgrazing (see Ling 2008) (this urchin did not occur on the experimental patch reefs from Chapter 4 due to their positioning on sandy substrata and isolation from natural reefs). Indeed, I detected no obvious instances of herbivory of juvenile *E. radiata* throughout my field experiments.

Nevertheless, *E. radiata* habitats across eastern Australia and Tasmania has suffered extensive overgrazing from the urchin *C. rodgersii* (Ling 2008; Johnson et al. 2011). To the extent that urchin barrens are extensive and persistent habitats in these regions, replacing the formerly complex kelp habitats. Moreover, with warming ocean waters, the poleward range expansion of herbivorous fish, including *O. cyanomelas* and tropical species (e.g. Kyphosidae, Siganidae, Vergés et al. 2016), represent increasing threats to *E. radiata* habitats across Australia. Therefore, while facilitation via associational defence might be a potential component of *E. radiata* population dynamics, it was untested throughout this thesis and remains an interesting avenue for future research.

Nonetheless, the results herein indicate that the amelioration of physical stressors can have strong effects on population dynamics in environments that do not fit the traditional characterisation of high-stress habitats. They also demonstrate that even the relatively subtle amelioration of abiotic conditions in ‘mild’ environments (reviewed by Holmgren & Scheffer 2010) can have important implications for habitat stability when they influence demographic processes such as recruitment.

Complexities of stress-depth gradients

One major complexity in this discussion is that while light can be a stressor of kelp – both directly, and indirectly via stimulation of turf algae – it is also a necessary resource for photosynthesis. Indeed, the depth distribution of kelp (where suitable substratum is available) is limited by the availability of light for photosynthesis (Lüning & Dring 1979; Steneck et al. 2002; Graham et al. 2007). Although *E. radiata* is one of the deepest growing kelp (>90 m, Nelson et al. 2014), the species typically does not form dense canopies below depths of ~30 m, suggesting resource limitation. It follows that along a depth gradient from shallow to deep, population dynamics of *E. radiata* may transition from dependency on facilitation to dependency on access to sufficient resources for growth. Thus, replicated experiments examining juvenile-canopy interactions along a depth gradient could be used to reveal details of a 'facilitation gradient' in *E. radiata* dynamics.

Existing research might also yield insights into facilitation gradients in other kelp species, although caution must be exercised when making generalisations across regions. Data from California on *M. pyrifera* at depths of ~15 m suggests that the species' recruitment dynamics are largely influenced by access to abiotic resources (i.e. light), as juveniles rarely grow beneath the adult canopy (Dayton et al. 1984, 1992; Schiel & Foster 2015). However, in shallower environments, such as in Chile where *M. pyrifera* typically only grows between 3–10 m (Buschmann et al. 2004; Vega et al. 2005), juvenile *M. pyrifera* seem to recruit and grow preferentially beneath the adult canopy (Vega et al. 2005; Buschmann pers. comms.). Therefore, facilitation from the adult canopy may be more vital for juvenile *M. pyrifera* in shallower environments, and the importance of intraspecific facilitation dependent on environmental gradients (e.g. depth/light).

Habitat mosaics and dynamic density-dependence

For *E. radiata,* the complex balance between access to abiotic resources and amelioration of abiotic stressors is reflected in results from Chapter 4. In general, canopies of adult *E. radiata* at moderate density (i.e. the average local density) provided the most suitable conditions for micro- and macroscopic juveniles. However, macroscopic juveniles grew faster beneath canopies of sparser adult kelp, whilst areas beneath the densest adult canopies had the highest rates of recruitment and survival of microscopic juveniles. Of the juvenile life stages, the established macroscopic juveniles are likely the most robust (Kirkman 1981; Schiel & Foster 2006), which may explain why they managed to grow beneath sparse kelp canopies where ecosystem engineering by adults is lower. Although, it appears there are some trade-offs to this, as juveniles beneath sparser kelp canopies did experience higher mortality than those beneath canopies of moderate density (see also Toohey & Kendrick 2007). On the contrary, the microscopic life stages that are less robust, recruited and survived best beneath dense adult canopies where ecosystem engineering was highest and abiotic stressors lowest.

The implication of these patterns is that different densities of adult kelp may facilitate separate demographic processes in a similar manner to how variations in canopy density facilitate community richness. At any one time, intact kelp habitats consist of a mosaic of canopy-patches of different adult density (often linked to age of the canopy and/or time-since-last-disturbance), and with each canopy-patch supporting a different sub-canopy assemblage due to differences in successional processes and sub-canopy conditions (Kennelly 1987; Wernberg et al. 2005; Irving & Connell 2006; Flukes et al. 2014, Chapter 4). Thus, in addition to supporting different assemblages, these canopy patches might also support different demographic processes. It would be possible to explore this hypothesis by monitoring a constant location within an *E. radiata* habitat and examining temporal patterns of density-dependence between the adult canopy and the life stages of the juveniles. Moreover, it could be instructive to compare levels of recruitment, resilience and productivity between areas of kelp with the same mean density, but of different variance around this mean.

Accordingly, mosaics of canopy density might facilitate ontogenetic shifts in habitat requirements and improve overall habitat resilience. This idea is essentially an extension of the 'seed bank' phenomenon known to occur in many kelp, including *E. radiata* (Kirkman 1981; Kinlan et al. 2003; Schiel & Foster 2006). The seed bank describes the cohort of juveniles that exist in the sub-canopy in a state of retarded development awaiting improved conditions (such as increased light from the thinning/opening of the canopy) and that respond rapidly after canopy disturbance. Certainly, rapid recruitment of juveniles after canopy-removal was observed in Chapter 3 and has been observed elsewhere in *E. radiata* (e.g. Kirkman 1981; Flukes et al. 2014) and other kelp species (Johnson & Mann 1988).

This flush of recruitment following canopy-removal is often taken as a sign that canopy-juvenile interactions are effectively negative, that is, that the canopy inhibits juvenile recruitment (Dayton et al. 1984; Schiel & Foster 2006; Wernberg et al. 2010). While this is true to some extent – Chapter 4 illustrates the poor survival of transplanted macroscopic juvenile beneath dense adult canopies – we demonstrate that this response in *E. radiata* is life-stage specific and that overall, canopy-juvenile interactions have a net-positive effect on the population demography. Ultimately, this dynamic density-dependence and phenological decoupling of the microscopic and macroscopic juvenile life stages from the adult canopy may be an optimal evolutionary strategy to limit intraspecific competition for resources and enhance population stability and resilience in response to episodic disturbances (Kinlan et al. 2013).

In the future

Chapters 2 and 4 utilised plaster clod cards to demonstrate that reductions in patch size are likely to cause relative increases in sub-canopy water flow. However, using that methodology, it was not possible to explore absolute changes to sub-canopy water flow, nor to determine how flow

dynamics (i.e. turbulent *vs*. laminar) might change in degraded kelp habitats. The use of improved technology, such as Acoustic Doppler Velocimeters, represents one approach that may enable more thorough characterisation of sub-canopy hydrodynamics. The scant previous research (Eckman et al. 1989) suggests that hydrodynamics beneath stipitate kelp canopies are characterised by low turbulent flows and high particle retention. Hence, knowledge of sub-canopy hydrodynamics across a range of *E. radiata* patch sizes/canopy densities will improve understanding of propagule dispersal, retention and settlement in degraded kelp environments. Detailed measurements of sub-canopy hydrodynamics will also improve understanding of engineering of seawater chemistry by kelp assemblages (Britton et al. 2016), and of the benthic boundary layers into which kelp propagules settle and develop (Chapter 5).

Overall, given the difficulties in working with the microscopic life stages *in situ*, relatively little is known is about dispersal and settlement dynamics of *E. radiata* spores and gametophytes under field conditions (but see Reed et al. 1988; Graham 2003). Fine-scale genetic analyses of parentage is one approach that may overcome some of these difficulties and enable novel analyses of the dispersal dynamics in *E. radiata* (Coleman et al. 2009). Factors affecting post-settlement survival and development of the haploid gametophyte life-stage are also largely unknown. Throughout the experiments in Chapters 3 and 4, I attempted to assess how patch dynamics affect survivorship of outplanted gametophytes but was unsuccessful as rates of mortality were effectively 100%. However, it is this sensitivity that makes it critical to improve our understanding of the performance of kelp gametophytes in degraded environments and future-ocean conditions. Likewise, the dispersing and colonisation life stages may be critical to the resilience of kelp habitats, especially given the likelihood of density-dependent effects on the fertilisation and success of microscopic gametophytes (Reed 1990b; Schiel & Foster 2006). Better knowledge of these life stages is also essential given the forecast increase of turf algae habitats (Connell et al. 2013; Falkenberg et al. 2015) that are replacing and inhibiting kelp forests in many places globally (Steneck & Johnson 2014; Filbee-Dexter & Wernberg 2018).

The examination of successional patterns and process in *E. radiata* kelp forests also represent an exciting direction for future research, with attention paid to how facilitation of kelp development from other macroalgal species aid the resilience of kelp beds. Existing studies have highlighted the lengthy recovery times of *E. radiata* that often occurs after large areas are cleared of adult canopy (Kirkman 1981; Toohey et al. 2007). While the slow re-establishment of *E. radiata* is presumably due to the breakdown of the environment-engineer feedback, and possible Allee effects given the short effective dispersal distances of *E. radiata*, large cleared areas typically experience the rapid and opportunistic establishment of other macroalgae including species of *Carpoglossum, Cystophora, Enteromorpha, Sargassum* and *Ulva* (Kirkman 1981; Toohey et al. 2007, pers. obs.). These macroalgae, and especially the habitat-forming fucoids (Order Fucales, incl. *Carpoglossum* spp.,

Cystophora spp., *Sargassum* spp.) may be important early-colonisers of these degraded areas and a critical successional stage of temperate macroalgal communities (Toohey et al. 2007; Bennett & Wernberg 2014; Coleman & Wernberg 2017). It is unclear why fucoid recruitment is less inhibited in degraded environments than that of kelp, but the larger and more developed fucoid propagules may be capable of withstanding physical and chemical conditions in which the much smaller kelp propagules perish or fail to germinate (Chapman & Fletcher 2002; Schiel & Foster 2006). In Chapter 5, I observed that the fucoids *Carpoglossum costata* and *Cystophora* spp. were capable of colonising turf algae habitats where kelp recruitment was impaired. It was also clear that *Ulva* sp. – a relatively delicate understorey species of green-alga – was reasonably effective at inhibiting the formation of turf algae. As such, ecosystem engineering from these early-colonising macroalgae may sufficiently ameliorate the degraded conditions over time to allow eventual recruitment and re-establishment of the kelp canopy.

Kelp forest restoration

Human intervention and direct restoration of degraded kelp habitats may represent one management option for kelp forests into the future and can complement other forms of conservation (Gianni et al. 2013; Marzinelli et al. 2016; Evans et al. 2017; Johnson et al. 2017). An important caveat however, is that there is little point in attempting restoration if the initial stressor or disturbance has not been ameliorated or addressed. This has stark relevance to the restoration of many marine habitats, including kelp forests, where key agents of degradation include the persistent pressures from increasing ocean temperatures, overgrazing by range expanding herbivores, and eutrophication and pollution.

The results and experience gained from this thesis, and especially from the construction of the experimental kelp patches from Chapter 4, could be valuable to future kelp restoration efforts. Firstly, the importance of adult *E. radiata* to juvenile conspecifics cannot be overstated: juvenile kelp transplanted in isolation are unlikely to provide satisfactory restoration outcomes. As discussed previously, the provision of adult kelp at different densities may also deliver benefits to multiple life stages of juvenile kelp, and thus the restoration of dense kelp canopies should be attempted alongside areas of moderate canopy density. This should provide high levels of resilience and recruitment in newly restored areas, while natural thinning of the transplanted canopy over time should facilitate the growth of macroscopic juveniles in the restored sub-canopy. The results from Chapter 4 suggest that for *E. radiata* populations in Tasmania, and providing patch size is not compromised, that adult kelp density as low as 4 sporophytes per m^2 may be capable of maintaining demographic function. Critically however, this minimum effective density is closely interrelated to patch size, such that patch sizes below ~7.5 m^2 required greater densities of kelp to remain resilient (Fig. 6.1). Although, below areas of ~2 m^2, kelp patches were unsustainable irrespective of kelp density. This threshold of

minimum patch size for *E. radiata* in Tasmania is also supported from the results of Chapter 3, where only the kelp patches smaller than 2.7 m^2 (i.e. 0.1, 0.3 and 0.9 m^2) suffered demographic collapse. This response surface provides estimates of the minimum patch sizes and kelp densities required to sustain environment-engineer feedbacks and could provide tangible objectives for the creation and formation of restored *E. radiata* patches, with the aim of creating self-sustaining and stable kelp habitats.

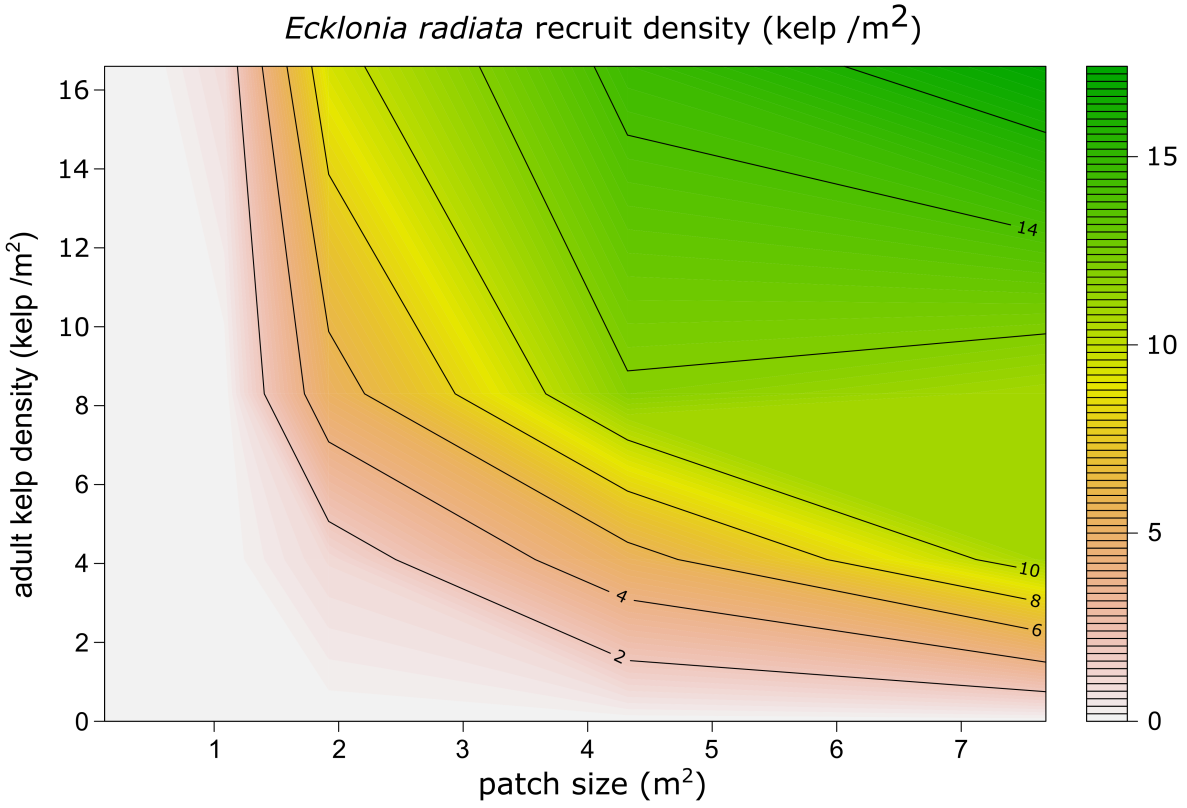

Figure 6.1 Response surface of the co-relationship between adult density and patch size necessary to maintain environment-engineer feedbacks and adequate recruitment, and thus patch stability of *Ecklonia radiata* in Tasmania. Estimated using recruitment and survivorship data from Chapter 4.

Overall, the results from this thesis illustrate that restoration of *E. radiata* ecosystems must focus on harnessing the internal processes that promote the stability of *E. radiata* habitats, through positive environment-engineer feedbacks (see also Suding et al. 2004; Halpern et al. 2007). For this reason, active intervention and restoration of *E. radiata* and other kelp might be best directed towards building resilience in existing kelp habitats and restoring areas that have suffered only minor levels of degradation. To this end, locations where adult kelp remain are the most promising for restoration, and so managers should focus on preventing further habitat loss rather than prioritising restoration of wholly denuded environments such as extensive turf algae habitats or urchin barrens (Johnson et al. 2017; Filbee-Dexter & Wernberg 2018). Furthermore, the resistance of these depauperate alternative states to kelp re-establishment (Gorman & Connell 2009; Johnson et al. 2017; Filbee-Dexter &

Wernberg 2018) – due to strong hysteresis in the system – means that the importance of maintaining the resilience of natural kelp habitats cannot be overemphasised. Ultimately, the management and conservation of kelp forests in the future should adopt policies that facilitate early-warning and intervention for kelp environments under threat, with the aim to restore resilience to these critically important habitats by harnessing their own internal stabilising mechanism.

Conclusion

In conclusion, while previous studies of habitat-forming ecosystem-engineers such as kelp have focussed on how external factors influence habitat dynamics, this thesis indicates that stability and resilience of these species can also be strongly influenced by internal processes. Ultimately, my results are consistent with the hypothesis that positive environment-engineer feedback facilitates the demography of *E. radiata*, and that changes to the local environment caused by adult *E. radiata* positively affects the demography of juvenile conspecifics (e.g. enhancing recruitment, survivorship, growth). These mechanisms can be characterised as intraspecific facilitation via an environment-engineer feedback. Crucially however, the impaired ability of *E. radiata* to engineer change due to reductions in patch size cause a breakdown in intraspecific facilitation and can lead to reduced habitat stability and resilience. The positive environment-engineer feedback of *E. radiata* occur through abiotic, biotic, and structural pathways. However, it is the structural pathway (i.e. the presence of the adult canopy) that is responsible for maintaining the strength and integrity of the abiotic (e.g. sub-canopy shading) and biotic (e.g. inhibition of turf algae) feedbacks. The implication of this for the management and conservation of *E. radiata* habitats into future is clear; the maintenance of intact adult kelp canopies will ensure the greatest likelihood of continued kelp recruitment and renewal of canopy cover.

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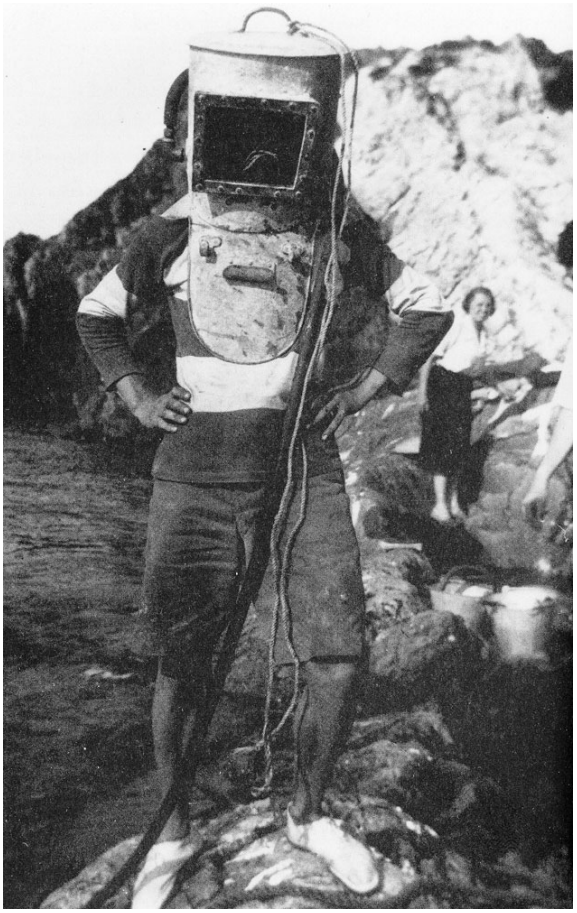

“Frequent diving led to a greatly increased appetite for sugar and treacle.”

Jack Kitching, 1934, while conducting some of the first scientific diving and subtidal ecological research